LAKE TURKANA

A REPORT ON THE FINDINGS OF THE LAKE TURKANA PROJECT

1972 - 1975

VOLUME 1

EDITED BY A. J. HOPSON

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LAKE TURKANA

A REPORT ON THE FINDINGS OF THE LAKE TURKANA PROJECT

1972-1975

GOVERNMENT OF KENYA AND
THE MINISTRY OF OVERSEAS DEVELOPMENT, LONDON.

EDITED BY A.J. HOPSON

Volume 1 of 6 Volumes

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VOLUME 1

Forward

Preface

Acknowledgements

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Chapter 2 Studies on algal dynamics and primary productivity in Lake Turkana

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LAKE TURKANA

FORWARD

For over 2,000 years the country lying to the south of the inhabited Nile Valley has been the subject of interest and speculation to the outside world. Travellers tales of the Great Lakes were possibly first recorded by Ptolemy in the second century AD, when he placed the source of the Nile in the high, snow covered Mountains of the Moon in Central Africa. Even so it was not until 1888, nearly 30 years after the era of the great Victorian explorers Baker, Burton and Speke, during which some half dozen of the Great Lakes of Africa were discovered by Europeans, that Samuel Teleki first set eyes on the "Jade Sea", and brought back reports of it to the western world. Since then the Great Lakes have become important providers of food, energy and water and our knowledge and understanding of them has been enhanced by careful scientific investigation over the years. Much of this work was done by British scientists closely allied with their local colleagues, and published by Her Majesty's Government in a series of predecessors to this present report.

Lake Turkana, as it now is, remote, mysterious, hidden in a most inhospitable region, has been the last of the great lakes of Africa, and indeed the world, to be studied in such detail. At the beginning of the work described here, even the depth of the lake was unknown for most of its area. The wildest speculations had been advanced on the possible yields of fish from it, and the Kenya Government were anxious to gain a better understanding of the true value of the lake. The study described by Mr Hopson and his team provides the biological and physical knowledge on which effective management policies can be drawn up, to ensure the wise and sensible exploitation of Lake Turkana for the good of the people of Kenya for many years to come.

Mr Hopson, who besides writing a number of the chapters himself, has edited the whole work, has suggested in his final chapter certain recommendations for the further development of Lake Turkana. The unemotional and factual way in which these recommendations are couched, in the proper scientific tradition, tends to conceal their exciting importance from the casual reader. The potential yield of over half a million tonnes per year of one tiny pelagic fish, once methods have been evolved to catch and process it, is perhaps the most attractive of these exciting possibilities. Again, the remarkable figures discovered by the team for the natural production of Sarotherodon in the Ferguson's Gulf area of the Lake, outstripping all but the most intensively fed and managed fish ponds, suggest a way to make enormous strides in tropical aquaculture throughout the world, once the factors responsible are properly understood. Finally, the most interesting and provocative, and possibly the most potentially valuable, of Mr Hopson's suggestions, is that some way should be found to minimise the enormous loss of energy and productivity which occurs in the Lake because there are no fish capable of utilising much of the blue green algae of the open waters, directly. This proposal would at one time have been regarded as controversial and speculative, but with increasing pressure on all Africa's natural resources we are beginning to recognise that wise and effectual management cannot afford to ignore the chance of such benefits.

The biological and bathymetric surveying of the great freshwater lakes of the world is now complete, and this report shows that Lake Turkana has given up its secrets at last. With the production of this report an era has come to an end, and never again will a team of young enthusiastic scientists be able to tackle a project of this size and complexity on a freshwater lake. It is fitting that these volumes should be printed and issued by the University of Stirling since the first of all bathymetric surveys, the classical treatise by Murray and Pullar on the Great Lochs of Scotland was initiated as a tribute to Pullar's son, drowned in what is now the central loch of the University of Stirling campus. Sir John Murray, the father of marine and freshwater biology, and himself a Stirling man, would indeed have been proud of the heirs to his traditions of scholarship. This exhaustive report is a tribute to the care and diligence with which the work was done and will prove of inestimable value to fisheries scientists, managers and planners both in Kenya and further afield.

J STONEMAN

Fisheries Adviser
Overseas Development Administration
London
December 1981

PREFACE

The purpose of this work is to present the detailed findings of the Lake Turkana project which was run and funded jointly by the Fisheries Department of Kenya and the Ministry of Overseas Development (now ODA), London. Proposals for the project were first discussed in Kenya in 1969 during a visit by Dr D N F Hall, the Fisheries Adviser to the Ministry of Overseas Development, and the Government of Kenya. Dr Hall was closely involved in the setting up of the project, and in the recruitment of staff and specification and procurement of equipment, particularly throughout the fieldwork and writing up periods, on behalf of ODA, and provided professional support and supervision for the team during this time.

Compared with other major African lakes, relatively little was known about the hydrobiology of Lake Turkana. Most of the available information was embodied in the reports of the 1930-31 Cambridge University Expedition which had concentrated on a localised area of the lake in the vicinity of Ferguson's Gulf and Central Island.

In 1969 the Kenya Fisheries Department was actively engaged in expanding the recently established commercial fishery on the lake. It was felt that in order to formulate policies for the management of the developing industry, detailed information was required relating both to the physical and chemical limnology of the lake and to the biology and population dynamics of the exploited fish.

The present project was therefore initiated with the object of carrying out a detailed multidisciplinary study of the entire lake with the following terms of reference:

(a) To complete an inventory of the species of fish in the lake, with particular emphasis on those likely to be of commercial importance.

(b) To study the ecology of the species likely to be of greatest importance in the commercial fishery.

(c) To determine the numbers of fish, and the growth rates, fecundity and other data relating to the different species required to define the nature and size of the maximum sustainable yield as well as the economically optimum yield.

(d) To determine the most appropriate means of catching the species of greatest economic importance.

(e) To prepare a chart or contour map of the lake.

(f) To study the limnology and and basic organic production of the lake, including a study to assess the effects on a commercial fishery, and the periodicity of long-term fluctuations in the lake level.

(g) The training of local counterpart staff to enable Kenya to continue to monitor the effects on the stocks, as fishing effort increases, after the project has finished.

The project leader made preliminary visits to the lake during October-December 1970 and again in May 1971 when he was accompanied by Dr D H Cushing of the Fisheries Laboratory, Lowestoft. In the course of the second visit, trials were carried out with a high-frequency echo-sounder to provide data required for the acoustic survey equipment which the Lowestoft Laboratory subsequently designed for the project.

A 50 ft steel research vessel was built for the project by the Campbeltown Shipyard, Scotland (see Main Appendix 2). The ship was finally launched into Lake Turkana from the shores of El Molo Bay on December 30th 1971 after a 4 week, 800 mile journey from the Port of Mombasa.

The survey team, which assembled in early 1972, was based at the Fisheries Station, Kalokol, situated about 3-4 km inland from the shores of Ferguson's Gulf on the west coast of Lake Turkana. A 750 ft air-conditioned laboratory, and living accommodation for a team of nine were specially built for the project by the Kenya Fisheries Department.

Field investigations started in March 1972 and continued until November 1975. Permanent members of the team were as follows. The number of months each worker was engaged in field work is shown in brackets.

P B Bayley	(24 months)	fisheries biology and statistics
A J D Ferguson	(30 months)	zooplankton, physical and chemical limnology
B J Harbott	(32 months)	algology, physical and chemical limnology
A J Hopson	(44 months)	fisheries biology and project leader
Jane Hopson	(30 months)	fisheries biology
J M Lock	(28 months)	fisheries biology
A A Q R McLeod	(44 months)	fisheries biology
A H S Mraja	(36 months)	fisheries biology (counterpart)
J E I Nockels	(24 months)	electronics engineer
J T N Ogari	(36 months)	fisheries biology (counterpart)
P Roberts	(16 months)	masterfisherman
L Smith	(22 months)	masterfisherman

A special feature of the project was the use, during 1974 and 1975, of the acoustic survey equipment alluded to previously. The gear, which was build specially for Lake Turkana, was operated initially in the field by staff on secondment from the MAFF Fisheries Laboratory, Lowestoft, where the original design work had been carried out. The following personnel were involved:

A J Burridge	(2 months)	electronics engineer
D Harding	(4 months)	fisheries biologist
S Lockwood	(4 months)	fisheries biologist
M J Pawson	(4 months)	fisheries biologist

The projects electronics engineer, Mr Nockels, carried out numerous modifications and refinements to the acoustic gear which have been described in a separate report (see Chapter 8 for reference).

Dr K Banister of the British Museum (Natural History) spent approximately six weeks at Lake Turkana during October and November 1973 carrying out taxonomic investigations of fishes on behalf of the project.

Overall responsibility for various aspects of the investigations has fallen to individual workers, but the arduous task of collecting field data has in many cases been shared by the entire team. Chapter 1 provides a detailed description of the physical and chemical environment together with notes on the recent geological history of the lake. The latter has an important bearing on the nature of the contemporary fish fauna. Algal ecology and primary productivity, on which fish - production is ultimately dependent for sources of energy, are considered in Chapter 2. Zooplankton and prawns, which constitute a particularly important link between the primary producers and fishes in Lake Turkana, form the subject of Chapters 3 and 4 respectively. Chapter 5 contains an inventory of fishes occuring within the lake and provides details necessary for the identification of adults and, in a number of cases, post-larvae. The commercial fishery is discussed at length in Chapter 6. Catch, effort and catch per effort are examined in turn and the selectivity of gillnets is also considered. Chapter 7 deals with the distribution and relative abundance of fish inhabiting the littoral regions of the lake. Surveys of open water fishes using various types of gear including trawls, townets, gillnets and acoustic gear are analysed in Chapter 8.

Patterns of distribution, both horizontal, and vertical, are demonstrated for numerous species of fish. Diel and long-term vertical migrapions are also studied. The results have been used in many cases to provide quantitative estimates of biomass. Detailed studies of the biology of the more important species are presented in Chapters 9, 10 and 11 which deal in turn with Cypriniform, Siluriform and Perciform fishes.

Chapter 12 examines the important role which zooplankton plays in the food chains of Lake Turkana. The work is concluded in Chapter 13 with a synopsis of the more important findings, followed by predictions of yield and a list of recommendations.

ACKNOWLEDGEMENTS

The survey team wish to express their gratitude to the Kenyan Fisheries Department, headed by the Director of Fisheries Mr Norbert Odero, for their substantial support during field investigations and for the excellent facilities, provided exclusively for the project, at the Ferguson's Gulf base. These included housing, laboratory and storage facilities as well as transportation and support staff. We would like to thank Mr Odero for his personal interest in the survey and in the trouble he took to overcome the many problems in administration, communications and supplies which cropped up as work proceeded.

As has been noted in the Preface, throughout the project team relied heavily on the advice and direction of Dr D N F Hall, Senior Fisheries Adviser, ODA, and we wish to record our appreciation of his support.

We are deeply grateful to Mr Robert McConnel, Fisheries Officer in charge of the Lake Turkana area, for the unstinting help he gave the project. We benefitted from the vast fund of experience he had built up during more than fifteen years service on the lake, and his willingness to provide sound advice and robust support contributed significantly to the success of the programme.

Junior staff played an essential role in the project and among many whose hard work and companionship we value, we wish to acknowledge particularly Mr Ndonji Musumba, coxswain of the research vessel; Mr Lewan Lengai, able seaman; Mr Enjoi Echapan, laboratory assistant; Mr Thomas Makuri, fisheries assistant and Mrs Rosalia Mwanzala, Secretary.

Help and advice came from many other quarters during the project, and we wish to extend our grateful thanks to the following:

Professor Leonard Beadle, a member of the 1929-30 Cambridge Expedition to Lake Turkana, who provided us with a wealth of background information and advice. He has also kindly allowed us to reproduce Figure 1.8 which originally appeared in Beadle (1974). Mr Noel Kenneway gave us the benefit of his long experience of the Southern end of the lake, gained during the same period.

Dr D H Cushing, Fisheries Laboratory, Lowestoft, who visited Lake Turkana during May 1971 in company with the project leader and gave expert advice on echo survey procedures and equipment.

Mr Derek Harding, Dr Steve Lockwood and Mr Tony Burridge all of the Fisheries Laboratory, Lowestoft, who were seconded to the Lake Turkana Project for periods of several months to assist in the setting-up and calibration of the echo survey equipment and the planning and implementation of echo surveys.

Dr P H Greenwood of the British Museum (Natural History) for advice throughout the project with problems of fish taxonomy and for the loan of the figures from Boulenger's "Fishes of the Nile" together with illustrations from his own work on *Haplochromis* reproduced in Chapter 5.

Dr Keith Banister also of the British Museum (Natural History) for help with fish collections and taxonomy during his visit to Lake Turkana in November-December 1973 on secondment to the project.

The Campbeltown Shipyard for the efficiency and care with which they constructed the research vessel R V HALCYON and in particular to their engineer Mr John Carmichael who spent six weeks on Lake Turkana re-assembling the vessel after its delivery in pre-fabricated sections from the Trench Point Yard, Campbeltown, Argyll.

Mr Dave Edwards of Express Transport who superintended the four-week journey of the 56 tonne research vessel carried by low-loader overland from Mombasa to Lake Turkana. He skilfully completed the last 300 miles of the route across virtually trackless rocky desert and organised the launching of the vessel into the Lake.

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The Kenya Police at Ilaret, who made accommodation available to field workers in an otherwise inhospitable region of the Lake.

The British High Commission, Nairobi which gave local administrative support on behalf of the Overseas Development Administration. The team are grateful for the sympathetic way in which their many problems were met and resolved.

During the final stages of the project, accommodation was made available in Britain at three institutions, for Team members to work up data and prepare their final reports. We thank the Director of the Freshwater Biological Association, Ferry House, Windermere and the Fisheries Laboratory, Lowestoft, also the Professor of Zoology, University of Liverpool for providing such facilities for periods of up to 20 months. We are also grateful to the Director of the Marine Biological Station, Port Erin, Isle of Man for allowing the team to use the library there.

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In completing these acknowledgements the authors wish to place on record their appreciation of the hard work, skill and enthusiasm of their colleagues Mr Lewis Smith and Mr Philip Roberts who were successive skippers of R V HALCYON and who were responsible not only for the operation and maintenance of the vessel but also the development, adjustment and upkeep of gear, much of it highly specialised. The success of the survey was also dependent on the services of our excellent electronics engineer Mr John Nockels who operated, maintained and also considerably refined the echo survey gear.

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Production of such a lengthy research report obviously requires considerable dedication from a wide range of people. The initial draft manuscript was typed with great skill and care by Mrs Angela Kneale of Port St Mary, Isle of Man. The major effort of production of the final word-processed text was carried out by Mrs Joanna Mackay with Mrs Laura Cumming, Mrs Anna Agius and Mrs Mary Ann Highfield, and art-work and diagrams were produced by Mrs Lyn North and Mr R B Stewart of the University of Stirling. The final editing and production of the report was carried out by Mr J Stoneman, ODA, Professor R J Roberts and Dr H P Stirling of the Institute of Aquaculture, University of Stirling, where the report was printed and bound.

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SUMMARY

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REFERENCES

1. GEOGRAPHICAL, PHYSICAL AND CHEMICAL ASPECTS OF LAKE TURKANA

A J D Ferguson and B J Harbott

INTRODUCTION

Lake Turkana* is situated in the north west of Kenya, in what was formerly the Northern Frontier District, within the co-ordinates 35°50' to 36° 40' East and 2°27' to 4°40' North. (Fig. 1.1 and 1.2). The northern tip of the lake lies in Ethiopia, close to the point where the Kenyan, Ethiopian and Sudanese frontiers meet.

The region is one of the most desolate and arid in East Africa and is served by few tracks and roads. The District centre, at Lodwar, is some 300 km from the nearest railhead at Kitale. (Fig. 1.2).

The country surrounding the lake is semi desert with a sparse vegetation of grass tussocks, thinly scattered bushes and stunted trees, the latter chiefly confined to the vicinity of dry water courses. The vegetation is usually dominated by the grass *Chrysopogon aucheri* (LIND and MORRISON, 1974). The dominant trees of open areas are *Acacia tortilis*. *A. nubica*, *Balanites aegyptiaca* and *Commiphora* spp. and, more locally, *Boswellia hildebrandtii*. In the vicinity of the larger water courses *Hyphaene* spp., *Pseudomussaenda flava* and *Salvadora persica* form dense stands. PRATT, GREENWAY and GWYNNE (1966), classified this type of land as 'very arid', class VI and of very low ecological potential with soil moisture indices of -51 to -57. (PRATT, 1970 after PENMAN, 1948).

Away from the lake, water sources are rare and often unreliable. Such a region is only suitable for nomadic pastoralists who are able to travel far in search of grazing and water for their flocks of goats, sheep, donkeys, cattle and camels. The principal tribe is the Turkana, after whom the lake is named. This tribe occupies an area of approximately 60,000 km^2, to the west and south of the lake, at a density of fewer than 3 people per km (OMINDE, 1970). As most of the available grazing is utilized by the Turkana, wild game is scarce or absent from most of the country west of the lake.

On the eastern side, however, a situation obtains where long-term hostilities, principally between the three main nomadic tribes, the Gabbra, Borana and Rendille, have contributed to the existence of an insecure, tribal no-man's-land. As a result, the area has remained relatively undisturbed by humans and their stock, and still supports a considerable population of arid-country game. In 1974, a large area on the eastern shore was gazetted as a National Park. (Fig. 1.3). In addition to its faunal and scenic interest, the area includes valuable palaeontological sites of early man. (COPPENS *et al*, 1976).

The region of the Omo delta, in the north, is settled by the Dasanech group of tribes who practice primitive agriculture, keep substantial flocks of animals, and fish in the branches of the river near the lake. The Merille, a division of this group, have, until recently, been involved in raiding down the eastern shore.

---

*formerly Lake Rudolf

The Samburu, an important tribe to the south east of the lake are present in large numbers around Mount Kulal and the springs at Loiyangalani. They are also traditionally a pastoral group. A small community of El Molo, meaning 'impoverished ones' or 'outcasts', survive through government aid and by fishing and keeping stock in the sheltered bays of the southeast lake.

EARLY ACCOUNTS OF THE LAKE

Reports of the existence of a large lake in the eastern rift valley of Africa first reached the notice of foreign travellers around 1880. (OLIVER and MATTHEW, 1963). Its discovery by Europeans, in March 1888, was described thus:

> "For a long time we gazed in speechless delight, spellbound by the beauty of the scene before us, while our men, equally silent, stared into the distance for a few minutes, to break presently into shouts of astonishment at the sight of the glittering expanse of the great lake, which melted on the horizon into the blue of the sky."

This was written by Lieutenant Ludwig von Hohnel (1894) in his account of Count Samuel Teleki's East African expedition, 1887-1888. Count Teleki named the lake after 'His Royal and Imperial Highness, Prince Rudolf of Austria', who had taken an interest in the plans for the expedition from its inception.

During the following thirty years, the region was visited by surveyors and occasional travellers whose accounts are reviewed by VON HOHNEL (1938) and BUTZER (1971).

Tribal and national unrest in the area discouraged more thorough investigations until the 1930's, when scientific observations were made by the Cambridge expeditions to the East Africa lakes (BEADLE, 1932; WORTHINGTON, 1932; FUCHS, 1934, 1935, 1939) and by ARAMBOURG (1933, 1935, 1943, 1948).

More recently, there have been sporadic and short-term visits to specific areas of the lake, notably by members of the East African Freshwater Fisheries Research Organisation (LOWE, 1954; HAMBLYN, 1961, 1962; MANN, 1964). Other groups include the Food and Agricultural Organisation of the United Nations (RHODES, 1966). Relatively little limnological work has been undertaken at the lake in recent years. However, detailed studies have been carried out on the geology, palaeontology and anthropology of the basin. The recent publication of "Earliest man and the environment in the Lake Rudolf basin". (COPPENS *et al*, 1976) brings together the wealth of information resulting from these investigations and forms an invaluable background to the fisheries-orientated research of the present study.

Apart from a few families and individuals traditionally catching fish in the lake, and small groups taught to fish by the District Commissioner (TRENCH, 1966), the Turkana were completely dependent on a pastoral economy. Severe droughts in 1960 and 1961 led to the setting up of famine relief camps near the lake and further inland, supporting thousands of starving people. In September 1961, the Government stationed a Fisheries Development Officer at Ferguson's Gulf (Fig. 1.3) primarily to provide these camps with fish.

The industry became organised on a commercial scale in 1963, and its subsequent development is documented in Chapter 6 of this report.

FORMATION OF THE LAKE AND THE PROCESSES LEADING TO ITS CONTEMPORARY STATE

DATING METHODS

Rocks, sediments and organisms considered in this section are mainly Plio-Pleistocene in origin, ranging in age from a few hundred to well over 5 million years*. The period is covered by geological dating methods with good overlap. Two main methods are used, C^{14} dating, reliable up to approximately 6 half-lives or ca 35,000 y b p, and the Potassium-Argon technique, for more ancient rocks older than ca 10,000 y b p.

Though a critique of dating methods is not within the scope of this paper, it is essential to remember their limitations. The radiocarbon method is based on the known decay rate or half-life of C^{14} and on the assumption of a constant C to total carbon ratio at the time of assimilation. The second assumption can be far from correct for in some lacustrine environments ancient limestones are undergoing erosion and the total carbon input into the environment thus has an abnormally low C to total carbon ratio. A further limitation is indicated by recent evidence from Bristlecone pine calibrations which suggests a general overestimate of the ages determined by the C^{14} method so that correction factors must be applied (see RALPH and MICHAEL, 1967, and SUESS, 1970a and 1970b for discussions of these and other limitations).

The decay of K^{40} involves accumulations, mainly of Ca^{40}, but also of Ar^{40}, and it is this build up of Ar^{40} which is the basis for a ratio-method of dating. While reliable for the most ancient of rocks, the method requires that the rock should have undergone no further thermal or chemical change since its original solidification. The solidifying process itself may take place over very long periods and the method is thus limited to wide, though clearly definable ranges, (DALRYMPLE and LANPHERE, 1969).

In spite of the possible inaccuracies of the techniques it is clear that the patterns of geological background to the region are well documented and verified by the best methods available.

GEOLOGICAL BACKGROUND TO THE LAKE SYSTEM

WALSH and DODSON (1969) carried out a detailed survey of the geology of the northern Turkana District, and reviewed many previous reports including those of ARAMBOURG (1933, 1935, 1943, 1948), FUCHS (1939) and DODSON (1963). Most of the following summary is based on YURETICH (1976), whose work includes more recent observations.

The basin is Cenozoic in origin and developed on Precambrian basement rocks. (Fig. 1.4). The basement rocks and granitic gneisses and amphibolites are believed to have metamorphosed between 1,100 and 450 m y b p. Little tectonic activity or sedimentation occurred in

*The abbreviation m y b p and y b p are used throughout this section for million years before present, and years before present, respectively.

the area during the Palaeozoic and Mesozoic eras, as it was apparently a high-standing depression between two major regions of uplift. (KING, 1970).

Formation of the rift valley system began during the Oligocene epoch, as evidenced by the oldest associated vulcanism. Most of these early associations of eruptive centres are located in the southern part of the eastern rift valley in Kenya and northern Tanzania (BAKER et al, 1972). The centre nearest Lake Turkana is Mount Elgon (Fig. 1.2) whose north-easterly slopes now drain into the Turkana basin via the rivers Bukwa and Suam. Ash production was significant at this time although lava flows were not volumetrically important.

A quiet period followed this initial outburst, during which bevelling of the topography occurred, seen today as the sub-Miocene erosion surface. It was not until the Miocene that actual downwarping of Northern Kenya began, and the formation of the present-day Turkana depression was initiated (BAKER et al, 1972). The first water-borne sediments, the Turkana grits, date from this epoch (WALSH and DODSON, 1969) and form a discontinuous basal sandstone which underlies many of the subsequent formations. The nature of the vulcanism changed during the Miocene to one dominated by fissure eruptions. Most of this activity occurred in the western half of the depression, associated with faults that have a general northerly strike. The rocks are largely alkali trachytes, with some basalts and basanites. This type of vulcanism continued into the late Pliocene.

FUCHS (1939) suggested that the lake lies in two grabens, separated by a narrow, shallower region off the mouth of the Kerio and Turkwel rivers. This hypothesis, based on evidence from the rifting of surrounding land, was substantiated by BOWEN (pers. comm. 1975). His analysis of the fault lines shown on echo-transects of the lake is summarised in Figure 1.5. The southern basin lies within the Gregory Rift Valley, while the northern basin occupies a subsidiary graben to the west. On criteria provided by HUTCHINSON (1957), Lake Turkana may be classified as a "type 9 lake".

The Gregory Rift Valley also contains the associated Stephanie and Suguta troughs (BROWN and VONDRA, 1973; FITCH and VONDRA, 1976; TRUCKLE, 1976; GROVE and GOUDIE, 1971). Both the northern and southern basins of the present-day Lake Turkana are relatively shallow compared with other African rift valley lakes, with maximum depths of about 84 m and 114 m respectively. (Fig. 1.14). The lake basin is the lowest point between the Ethiopian and Kenyan highlands.

The orogenic periods leading to the major uplift of the Ethiopian plateau are broadly synchronous with those of the Kenya Highlands (BUTZER, 1971). MOHR (1968) places the main rift faulting and updoming in the early to middle Miocene, with at least two phases of renewed uplift during Plio-Pleistocene times.

Copious lava flows were a conspicuous feature of Pleistocene volcanic activity. Most of this activity took place to the north of the Ethiopian plateau, but significant amounts of Pleistocene to Holocene lava were deposited around the lake (Fig. 1.4), (YURETICH, 1976). These lavas are primarily basalts, although there are associated silicic differentiates. Such recent basalts are a prominent feature at the southern end of the lake. It appears that before this period, the lake extended further south into what is now the Suguta trough (Fig. 1.5) and that the formation of a barrier of Pleistocene lava cut off the trough from the main lake. (CHAMPION, 1937).

PAST CONNECTIONS BETWEEN THE OMO-TURKANA AND NILE BASINS

Introduction

Zoogeographical evidence strongly suggests that the Omo-Turkana basin has been, at times, directly connected with the Nile basin. Rocks in the most ancient Omo basin (see later), contain the remains of at least seven species of molluscs and eight species of fish common to the Nile system today. (ROGER, 1944; BUTZER, 1971). From about 4.4 to 1.81 m y b p, a nilotic fauna was distributed throughout the subsaharan zone. The ichthyofauna of the modern lake is essentially nilotic with only 7 endemic species out of a total of 47.

Geological indications of overflow levels attained by the lake during its development provide further evidence. BUTZER (1971) has carried out a detailed study of the lower Omo basin and delta, which throws light on the changing lake as a whole.

The Omo plains are nowadays separated from the Lotagipi Swamp, to the west, by a low-level divide about 450 m. a s l, this divide was the site of connection with the Nile basin.

Sedimentary history

PATTERSON et al (1970), found that early Pliocene sediments at Lothagum (see Figure 1.3) were accumulating from both lacustine and riverine environments. On the basis of this evidence, BUTZER (1971) suggests that the lower Omo basin was created along modern lines at this time and that a lake has existed continuously in the basin from ca 5 m y b p to date. During this time, the lake has undergone many major changes in size, water chemistry and depositional environment.

Plio-Pleistocene sediment sequences indicate the Omo river-mouth to have been between 90 and 120 km north of the present delta fringe (Fig. 1.7). The Nkalabong formation, dating from ca 3.9 m y b p was formed during the highest late Coenozoic transgressions and may indicate a lack of torrential runoff. Other deposits in the 'Omo beds' group show the presence of an intermediate delta ca 50 km north of the existing delta. These movements of the delta fringe may indicate apparent climatic changes, although some alteration of tectonic deformation probably occurred. Geologic and geomorphic evidence suggests a semi-arid climate throughout the late Coenozoic.

The youngest 'Omo beds' were faulted between 1.81 million and 130,000 y b p, during the lower to middle Pleistocene. This was followed by renewed sedimentation to the west of the modern delta. BUTZER (op. cit.) suggests the present structural patterns of the basin were established after this time.

A mid-Pleistocene to mid-Holocene span is represented by the littoral, deltaic and fluvial beds of the Kibish formation (Fig. 1.7) to the northwest of the current Omo plain. These units date from ca 130,000 to 3,000 y b p. The most ancient of the Kibish units indicate a lake level between 60 to 70 m above 1970 levels, and that the Omo delta was further north, with tenuous though real connections linking the Omo-Turkana and Nile basins.

No deltaic or littoral records from between 35,000 and 9,500 y b p have been found in the Omo basin, but it is likely that the lake was low, with arid conditions prevalent. BUTZER et al (1972) state that carbonate horizons and desert varnish on lag pebbles are associated with this phase.

Dates of the latest period of connection with the Nile system can only be determined from wave-cut beach lines at elevations sufficiently high to allow overflow through the Alabilab and Lotagipi swamps to the Pibor-Sobat river systems. Such overflow occurred between 9,500 y b p and 7,500 y b p, when the lake was close to 60 to 80 m above its present level (60-80 m +) (BUTZER, 1971). This was followed by a drier period during which the level fell very rapidly until the lake was closer to its contemporary margins. Approximately 6,600 y b p, the lake surface was only ca 15 m + but rose to between 65 and 70 m +, by 6,200 y b p. This level was maintained until after 4,400 y b p, when the lake dropped slightly before reaching its final high stand of 70 m + around 3,500 y b p. It is not clear whether or not real connections were effected with the Nile between 6,200 y b p and 3,500 y b p, although the levels were probably high enough to flood the Alabilab and Lotagipi swamps periodically.

RICHARDSON and RICHARDSON (1972) point out that this last 'pluvial' period affecting Lake Turkana was more recent than those of rift valley lakes which received runoff from areas other than the Ethiopian Highlands.

Area of 'Mega Turkana' at times of connection with the White Nile

BUTZER (1971) attempts to describe the low divide to the northwest of the modern lake, and to quantify the altitudes involved. It is evident, however, that the southeast corner of Sudan lacks definitive topographical mapping, and that the surface of the lake was used as a reference datum for all observations. All descriptions must therefore remain tentative until absolute elevations have been determined.

Using mainly the 1:250,000 series Y-501 of the Survey Office, Khartoum (1941) sheet numbers 78-L and 78-P, a probable line of connection is suggested here.

A complex area of low plains and swamps bordered by steep scarps of over 640 m. a s l lies between the Pibor-Sobat rivers and modern Lake Turkana. Surveys by AUSTIN in 1901, WALLER in 1909, and WAKEFIELD in 1938 form the basis of sheet 78-L and describe this region. Water probably flowed via the Alabilab and Lotagipi swamps (Fig. 1.6), thence northwest through "a flat valley, muddy in the wet season" (ATHILL, 1920), to the Nile tributaries.

Though reliable information on the topography is scant, an attempt has been made to define the possible limits of the lake during periods of connection with the Nile.

The Y-501 series (1941), FUCHS (1939) and War Office and Air Ministry, London, series Y-633, edition 1 GSGS (1960) maps combine to indicate the involvement of a sill at ca 130 m above modern lake level. This is ca 55 m above the maximum height suggested by geological evidence, but it was used to construct a contour line which would represent the largest area that might have been flooded. Serious discrepancies and inaccuracies in the early topographical mapping could easily account for the differences in elevation noted here.

It is estimated that Mega Turkana could have covered a maximum area of 32,890 km at times of overflow. While at this level, wave-cut beach lines were left which provide obvious pointers to contemporary observers (Plate 1.1). WALSH and DODSON (1969) review the formation of these features.

YURETICH (1976) estimates that this maximum area was 38,500 km although his value is determined from a map which includes much of the Suguta trough (Fig. 1.5). The trough was almost certainly separated from the main lake by the time Lake Turkana last overflowed (CHAMPION, 1937; TRUCKLE, 1976) but did not become permanently dry after separation. Lake levels in the valley attained a maximum of ca 600 m. a s l around 9,660 y b p. This is about 235 m above the surface of modern Lake Turkana, and 155 m above the level of Mega Turkana. The lowest point on the barrier between the basins is ca 834 m. a s l (TRUCKLE, 1976).

Both CHAMPION (1935) and TRUCKLE (1976) report the remains of nilotic fish in and around the Suguta swamp indicating a former more permanent water body in the region and an earlier connection with the main lake. The Suguta and Stephanie depressions (Fig. 1.5) formerly held persistent water bodies but now contain water only after heavy local rain (GROVE and GOUDIE, 1971; TRUCKLE, *op. cit.*).

The culmination of the last glaciation, around 19,000 y b p corresponded to a period of aridity in the tropics. A date of 14,750 - 290 y b p has been attributed to the initial retreat of a glacier in the equatorial Ruwenzori mountains of Uganda (WHITTOW and OSMASTON, 1966) and full interglacial conditions existed in higher latitudes by ca 10,000 y b p (STREET and GROVE, 1976).

In 18 out of 20 cases, major water bodies in Africa, including Lakes Chad, Victoria and Turkana, attained their maximum post glacial levels between 9,500 and 9,000 y b p (STREET and GROVE, *op. cit.*), while the now extinct Saharan lakes covered large areas (BEADLE, 1974). Rift Valley lakes in Ethiopia similarly reached high levels at this time (WILLIAMS *et al*, 1977) and reflect parallel climatic changes.

The contemporary Lakes Nakuru and Elementaita were joined and Lake Naivasha was overflowing (KAMAU, 1972; RICHARDSON and RICHARDSON, 1972). BUTZER *et al* (1972) graphically summarises the changes in certain African lakes presently occupying closed basins and BEADLE (1974) adds information on Lake Victoria to the same figure which is reproduced here (Fig. 1.8).

RECENT CHANGES IN THE LEVEL OF LAKE TURKANA

BUTZER (1971) reviews and rationalises sedimentary, written and photographic evidence of changing lake levels during the last 90 years, primarily to clarify the temporal basis of submergence-emergence patterns in the Omo Delta region.

Figure 1.9 summarises the fluctuations. The basic pattern is of a falling lake level shortly before 1888 (Fig. 1.10) followed by a rise to a maximum, 15 m above the present level, in 1896 (Fig. 1.11). The level then dropped rapidly by 13 m in the period up to 1908, after which the evidence indicates a rapid rise of at least 3 m around 1918 (Fig. 1.11). Sanderson's Gulf, the large tectonic depression lying to the north of the Labutt range, west of the Omo Delta, then became separated from the main lake and was subsequently reconnected only during the highest levels. From the early 1920's, the level continued to fall gradually until 1954, when it was approximately 5 m lower than that recorded in 1970 (Fig. 1.12). Heavy rains during 1961 and 1962 caused Lake Turkana to rise ca 4 m, re-connecting Lakes Nagum and Fadja to the main lake (Fig. 1.12) and forming a shore line which persisted relatively unchanged into this decade.

From early in 1949, the Water Development Division, Nairobi, investigated monthly gauge readings at Ferguson's Gulf. These continued until 1962, when the gauge was submerged, and records do not start again until 1966. Thereafter, readings appear to have been irregular, and it is only by interpolation and the use of geomorphological evidence that BUTZER (1971) has extended the curve (shown in Fig. 3-6, p 123) to include all the information from 1888 to 1970. The present study includes data from three gauges in Ferguson's Gulf, starting in October 1971. Readings from these are used to up-date BUTZER's records and it is clear that during the subsequent five years there has been a net fall in lake level (Fig. 1.13).

Lake Stephanie, to the northeast (Fig. 1.5) has shown trends essentially similar to those of Lake Turkana, being high in 1888 but dry from 1898 to 1961, only filling towards the end of that year. Thereafter, the lake shrank to become an expanse of dry flats, holding water only after heavy rain to the north (BUTZER, 1971; GROVE and GOUDIE, 1971; pers. obs. 1974).

RECENT CHANGES IN THE LEVEL OF OTHER AFRICAN LAKES

Parallels between the fluctuations in water level of lakes in central and east Africa can be drawn from more recent records as well as from ancient geological evidence. STREET and GROVE (1976), summarise the situation in Africa as a whole. They point out that the dry climate of the last 2,000 years has been interspersed with minor, moister fluctuations around 100 year cycles, while during the present century, lake levels have oscillated widely over 10 to 30 years. Most African lakes are reported to have attained high states from 1870 to 1895 and again from 1950 to 1965.

More specifically, the fluctuations of Lake Tankganyika have been chronicled by LAMB (1966) thus:- low in the first half of the 19th century, high between 1874 and 1879, low from 1895 to 1960 with minimumlevels in the 1920's and between 1948 and 1956. The low stand of 1960 was ended by a rise of ca 3 m. He also reports a rise in the level of Lake Victoria from 1878 to 1879, a drop in the 1880's, followed by a recovery to an intermediate level in 1892 to 1895. High levels were attained in 1906 and 1917, thereafter falling to a minimum for (as were most of these transgressions) by direct rainfall onto the lake surface (FLOHN and FRAEDRICH, 1966; LAMB, 1966; MORTH, 1967).

Lakes in the eastern arm of the rift valley, in Kenya, show similar trends. In 1930 and 1931 levels of Lakes Nakuru and Elementaita were approximately 7 m higher than in 1957. Later, during wetter years beginning with 1961, sharp rises were recorded for Lakes Naivasha, Nakuru and Elementaita (RICHARDSON and RICHARDSON, 1972). Gauge readings on Lake Naivasha registered a fall from 1938 to 1946 and a sharp rise from 1961 to 1964 of ca 3 m.

Fluctuations in the level of Lake Turkana since 1888 parallel those of Naivasha (BUTZER, 1971; RICHARDSON and RICHARDSON, 1972).

CONTEMPORARY PHYSICAL FEATURES

BASELINE DATA

Fluctuations in the lake level result in marked alterations to the shoreline, which obviously make definitive mapping difficult. The outline as of 10 September 1972 has been chosen as the basis for plotting all subsequent information on lake changes. This map (Fig. 1.14) was constructed from series Y-50, edition GSGS Survey of Kenya maps, and supplemented by information from Earth Resources Technology Satellite* photographs taken on 10 September 1972.

The lake level on the same day has provided a datum for the depth contours in the bathymetric chart (Fig. 1.14). This chart was based on a series of echo-transects carried out from R V HALCYON between March and August 1972, using the Ship's Kelvin Hughes MS 44 echo-sounder.

Accurate information regarding the absolute height of Lake Turkana above sea level is not available. However, the most recent and probably the most reliable measurement was obtained by the Ministry of Defence, UK, on 22 June 1972, at the south end of the lake, near Loiengalani. This estimate, based on reciprocal trigonometric levelling from benchmarks of known height lying to the southwest of the lake, indicates a surface elevation of 365 ±5 m above mean sea level at Mombasa. As the lake level rose 40 cm between 22 June and 10 September 1972 (Fig. 1.13) the level at that date has been taken as 365.4 m ±5 m a m s l. This figure has provided a base point for all subsequent lake level gauge readings, and is regarded as the zero reading for the period of study. The table of physical dimensions (Table 1.1) similarly relates to the situation for September 1972.

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*The abbreviation ERTS is used in the subsequent account.

CLASSIFICATION OF LAKE REGIONS

The open water has been divided into four sectors to aid locational description (Fig. 1.15). Physical and limnological features provide the basis for this classification. Two major inshore regions, the Omo Delta and Ferguson's Gulf, are considered separately.

(i) The Northern Sector

The northern basin is relatively shallow and slopes very gradually to a maximum depth of 35 m north of North Island. The slope from the Omo delta to the deepest part is about 1 in 1600.

(ii) The Central Sector

This basin is deeper and is almost symmetric, sloping to a maximum depth of 84 m in the middle. The symmetry is interrupted by Central Island and by the steeper slope of the lake bed in the vicinity of Jarigole (Fig. 1.3) where a major fault line lies adjacent to the shore.

(iii) The Turkwell Sector

This area of relatively shallow water, with a maximum depth of less than 40 m separates the two major basins. The Kerio and Turkwell rivers flow into a large bay forming much of the western shore.

(iv) The Southern Sector

The southern basin is the deepest part of the lake, with soundings of 114 m to the south of South Island. The surrounding terrain is mountainous and the lake bed generally shelves steeply from the shore.

(v) Major Inshore Areas

(a) The Omo delta

The recent history of the Omo delta has been described in detail by BUTZER (1971). Figure 1.16 shows the comparatively minor changes which took place during the present study.

Two major distributaries were active during the study period. The Dielerhiele arm forms a long sinuous channel which is bordered by levees and extends about 15 km into the lake, terminating in a delta fan. The Erdete branch is similar but is shorter and has a smaller delta fan. During recent years, the Murdizi branch of the river, which lies in the north east corner (Fig. 1.12) has become extinct.

Prior to the transgression of 1961-1963 when the lake level rose ca 4 m, two large shallow lakes, each of 30-40 km^2 , Lakes Nagum and Fadja, were situated in the delta. Subsequent flooding involving about 400 km^{2}of low-lying land has led to their incorporation with the main lake.

(b) Ferguson's Gulf

WORTHINGTON (1932) provides a map of Ferguson's Gulf which was made during the period December 1930 to January 1931. Outlines from RAF photographs taken in August 1958 and January 1972 have been superimposed on the 1930-31 map to illustrate changes which have taken place in the shape of the Gulf. The changes are attributable to a combination of varying lake levels together with erosion and deposition by wind and water currents. Within the Gulf, most changes have been caused by variations in lake level. On the inner side of the spit, where the bottom shelves steeply, the shoreline has remained relatively stable. An extensive area of mud flats bordering the west shore of the Gulf leads to a rapid alteration in outline with relatively minor changes in lake level.

The effects of erosion are most clearly seen on the outer edge of Longech Spit, which is exposed to the prevailing south easterly winds (see later, page 18). Figure 1.17 shows that the width of this promontory has decreased by 50% between December 1930 and January 1972, a mean rate of about 20 metres per year. As mentioned previously (Fig. 1.9) the lake levels at these dates were probably very similar.

During the high lake levels prevalent since 1963, the sand ridge at the northern tip has been subjected to heavy erosion during infrequent storms from the north.

The situation in the Kalakol delta area (Fig. 1.17) is complicated with depositions of riverine sediments counteracted by strong northerly currents along the west shore. During the past 40 years, the net effect has been a retreat of the shoreline of approximately 800 m at the Kalakol river mouth.

Changes in the shape of the southeast corner of the Gulf can be attributed to wind-blown sand from the crest of the high coastal dune ridge being deposited in the Gulf. WALSH and DODSON (1969) had previously noted this feature, and the aerial photograph in Plate 1.2 clearly shows dune movement into this area.

Fluctuations in the level of the lake have been accompanied by marked variations in the area of Ferguson's Gulf. This is illustrated by the areas calculated from various sources sho in Table 1.2 which, when plotted against the depth (Fig. 1.18) show a relatively straightforward relationship. When the maximum depth of the Gulf exceeds 4.5 m, the western margin is limited by sand dunes and the rate of increase in area becomes reduced. It is interesting to note that the area and volume calculated from WORTHINGTON's 1932 map agree with our findings.

The bathymetric maps shown in Fig. 1.19 illustrate several interesting features. It is evident that the complexity of the Gulf's entrance has increased since WORTHINGTON's survey and between April 1973 and April 1975. This is probably due to the deposition of material eroded from Longech Spit and brought to the entrance of the Gulf by the currents illustrated in Plate 1.2. It is also evident that the Gulf decreased in depth between the two surveys of April 1973 and April 1975. Gauge readings

(Fig. 1.13) show a net fall of about 0.7 m between April 1973 and April 1975 but the bathymetric surveys indicate a decrease in depth of about 1 m between these dates. The actual decrease in depth remains uncertain due to the possible errors in the surveys but considerable quantities of sediment were observed to be entering the Gulf during heavy flooding of the Kalakol river in April 1973 and again in April 1974.

THE CATCHMENT AREA

Lake Turkana, like many other desert lakes (COLE, 1968) relies on rainfall in distant upland areas. Local precipitation is totally inadequate to maintain the lake level.

A summary of the physical characteristics of the catchment area is given in Table 1.3. Estimates made during the present study are in general agreement with those of BUTZER (1971) and YURETICH (1976). For convenience the catchment area of Lake Turkana has been divided into three sections (Fig. 1.20). The geology is shown in Figure 1.4.

Section 1 - Omo basin

Over 90% of water flowing into the lake originates from the Omo basin although this region forms only 58% of the total area. Most of this water is derived from a limited area in the Ethiopian Highlands where rainfall exceeds 150 cm per annum (GRIFFITHS, 1972a). Records for Jimma (07 $^{\circ}$ 39' N, 36 $^{\circ}$51' E, 750 m a s l) situated in the highland region indicate that rain principally falls between April and September, with a maximum monthly mean of 23.1 cm in July. There is a three month lage between the onset of seasonal rains in the highland catchment area and the resultant increase in the lake level.

The duration of the flood period and the increase in lake level depends mainly on the amplitude of the seasonal rains in the Omo catchment area. BUTZER (1971) showed that the lake transgression of 1961-63 resulted from the prolongation of the rain season combined with increased precipitation. However, he was unable to find any correlation between rainfall at stations in the Ethiopian catchment area and fluctuations in lake level. This is probably due to the local nature of many of the rainstorms in an area where data collection stations are few.

The geology of the highland areas of the Omo basin studied by MOHR (1971) and summarised by YURETICH (1976) is of particular relevance to the present investigations since it determines the mineralogical and chemical characteristics of the sediment load. Table 1.3 shows that the majority of rocks in the Omo basin are volcanic in origin with Precambrian rocks (mainly quartzite and amphibole schists) present in only 7% of the area.

The volcanic rocks have been divided into two groups of different ages which have somewhat different characteristics. The most extensive of these are the Magdala group of Miocene-Pleistocene basalts and rhyolites which dominate the upland areas. The rhyolites are 'acidic' having a relatively high proportion of silicate. These rocks are also relatively rich in sodium and potassium but poor in calcium. The lower series of basalts are called the Achangui series and are mainly 'alkaline' olivine basalts which are relatively poor in silicate, but have a higher proportion of iron, magnesium and calcium components.

Section 2 - The Kerio-Turkwell basin

The Kerio and Turkwell rivers provide less than 10% of the total water discharge into the lake, although their drainage basin forms 28% of the catchment area.

Precambrian basement rocks with a high soda and potash content (YURETICH, 1976), predominate (Table 1.3). They are composed mainly of biotite and hornblende gneisses (rich in magnesium), migmatite and plagioclase amphiboles (PALLISTER, 1971). In the Kerio valley extensive areas of olivine basalts are interspersed with the basement rocks.

Section 3 - Ephemeral rivers

Numerous minor ephemeral water-courses drain into the lake from the surrounding country. These flood during infrequent and short-lived rainstorms. They flow intermittently, often only once yearly for a few hours at a time, and are only of local importance. In terms of water and sediment input to the lake as a whole, their contribution is negligible.

The geology of the areas drained by these rivers is complex and has been well studied on the west side by CAUKWELL (1938), FUCHS (1939), WALSH and DODSON (1969) and, in the south, by DODSON (1971).

Lacustrine deposits near the lake to the north of Allia Bay have recently attracted the attention of geologists but there are so far no reports on the geology of the terrain further inland. The area which extends from Allia Bay to the south end of the lake awaits detailed investigation.

To the west of the lake, north of the river Turkwell, most ephemeral rivers rise in basaltic hills and subsequently flow for distances up to 12 km across coastal plains, formed by old lacustrine deposits, before reaching the lake shore. These ancient lake beds were exposed during the post-Pleistocene regressions.

At the northern end of the lake, the Laburr hills lie close to the west shore. These hills include basement rocks as well as semi-pelitic gneisses and crystalline limestones (WALSH and DODSON, 1969). The more extensive area of basement rocks forming part of the Loriu Range on the south west coast between Kalamongin and Luguruguru consist of biotite gneisses similar to those of the Turkwell-Kerio basin (DODSON, 1963). Rivers in this region run straight off the steeply sloping basement rocks into the lake without passing through old lake deposits.

From the south west corner to the north of El Molo Bay, the rocks consist mainly of Pleistocene basalts (FUCHS, 1939). The runoff in this area is probably the lowest for the whole lake. The coastal plain from El Molo Bay to Moite is formed of lacustrine deposits with basalts further inland. A small area of basement rocks occurs near the coast north of Porr (FUCHS, 1939). Runoff from Moite, an isolated mountain of byenite (Dr C SWAIN, pers. comm.), may have led to the local differences in the trace element composition of the sediments found in this area by YURETICH (1976). Between Moite and Allia Bay ephemeral rivers drain directly from a range of basaltic hills into the lake.

From Allia Bay northwards the lake is bounded by coastal plains up to 35 km wide chiefly of recent lacustrine deposits. In many instances however, the water courses have cut down into older lacustrine or fluvial beds dating back to at least 4.6 m y b p (VONDRA et al, 1970).

The location of four permanent springs observed flowing into Lake Turkana is shown in Figure 1.3. Discharge from these sources is negligible and their effect on the lake environment is extremely localised. Chemical analyses are presented later in Table 1.13-1.15.

THE LAKE BED

Topography

The general topography of the lake is evident from the bathymetric map (Fig. 1.14) but detailed information on features shown by echosounder traces is considered here.

The Northern Sector

Echo traces from the northern sector show that most of the lake bed in this region is relatively flat with few fault lines (Plate 1.3). The plate also illustrates the effect on more turbid water from the River Omo on a midwater scattering layer, the significance of which is discussed in detail later (see page 17).

Plate 1.4 illustrates a type of trace encountered solely in the vicinity of Kakoi and at a depth of 20-30 metres. The significance of the series of depressions in the lake bed is unclear but they might represent part of a submerged deltaic system of channels. The bottom deposits were invariably of sticky mud which tended to hinder bottom trawling. Mud of this consistency occurred rarely in other areas.

The Central Sector

Plate 1.5 shows an echo trace obtained on a course from Ferguson's Gulf to Central Island. The lake bed shelves steadily offshore to the 30 m contour where a sudden increase in depth indicates a major fault line. This is followed by a second fault line with depth increasing rapidly from 48-60 m. The transect ends with the bottom profile rising steeply at the edge of a submerged crater on the north coast of Central Island.

The form of the graben in which the northern basin of the lake is situated, with its associated fault lines, is demonstrated in Plate 1.6 which shows an echo-transect following a line running due west from Koobi Fora. The trough which appears on the fault in the western half of the transect is a type of structure which was noted relatively frequently in association with fault lines.

Koobi Fora Spit is a prominent feature on the eastern shore of the Central Sector. The bathymetric survey revealed that from the tip of this promontory, a strip of shallow water extended westwards more than 3 km into the lake. Plate 1.7 illustrates the transverse profile of the spit in an area approximately 2km offshore. The south face of the spit forms a steep escarpment with the bottom shelving from 4 m to 23 m in a distance of only 90 m. This declivity is probably maintained by strong currents. Similar sand spits are found on the eastern shore of Lake Mobutu (formerly Lake Albert).

Turkwell Sector

The bottom in this sector is relatively level and featureless with few fault lines. Traces shown in Plates 1.8 and 1.9 illustrate the more unusual structures. North west of Sandy Bay echo traces indicate that the generally level bottom was interrupted by frequent shallow depressions (Plate 1.8) similar to those observed near Kakoi (Plate 1.4). However, in the Turkwell Sector the superficial layers of soft mud overlay a deeper body of harder material. Such hard material, almost certainly rock, forms a submerged reef situated in the centre of the lake west of Porr (Plate 1.9). The reef rises approximately 9 metres above the surrounding muddy bottom. Apart from a submerged peak observed ca 2 km west of the satellite islets of Central Island, this reef was the only structure of its kind noted in the offshore waters of Lake Turkana.

The east shore of the Turkwell Sector is interrupted by a numbe of moderate sized sand spits, the largest of which forms the outer arm of Sandy Bay. As with Koobi Fora and Moite spits, echo survey has proved that these promontories extend below the surface well offshore. Figure 1.10 shows an echo trace recorded on a line starting from Sandy Bay and running parallel to the coast in a south-easterly direction approximately 1 km offshore. Sections of two submerged sandspits appear.

The Southern Sector

Bottom topography in the Southern Sector is more varied than elsewhere. Plate 1.11 shows the uneven nature of the lake bed on a course between Loiengalani and El Molo Bay. This is typical of inshore areas near rocky shores throughout the sector. The deep trough south of South Island is similar to the main basin of the Central Sector with a relatively smooth bottom shelving down in a series of steps resulting from faulting. North of South Island extensive areas below the 40 m contour are generally level and featureless.

Substrate

Sediment description

The bottom of Lake Turkana consists principally of soft sediments and rocky substrates form less than 5% of the total area.

A detailed study of the sediment was carried out by YURETICH during 1973 and 1974 using coring equipment deployed from R V Halcyon, supplemented with samples collected by anchor dredge and Eckman grab. In 1973 a gravity corer was used to take 1 m cores and in 1974 3 m cores were obtained with the aid of a piston corer. A total of over 100 samples were obtained from sites throughout the lake and subsequently analysed at the Department of Geology, Princeton University. Results are presented in a PhD thesis (YURETICH, 1976) which provides a wealth of information on the physical and chemical environment, on the geological history of the lake and on processes involved in the formation of minerals in the sediments.

The average composition of sediments in terms of particle size and mineral composition is shown in Table 1.4. Relative proportions of different size fractions are similar to many other lakes but mineral composition is unusual in this respect. The montmorillonite-kaolinite-illite composition of the clay fraction in the Lake Turkana sediments has been recorded only rarely elsewhere and the proportion of carbon in the sediments (0.63%) is extremely low. Lake sediments usually have a much higher proportion of organic compounds in the form of gyttja or sapropel.

Significant differences in the mineral and chemical composition of sediments were noted in Lake Turkana from area to area (Fig. 1.21). These have been attributed to local variations in the proportion of constituents derived from each of the various riverine catchment areas. The principal source of the lacustrine sediments are the volcanic rocks of the Omo Basin. This northerly input is reflected in a marked decrease in concentrations of iron, titanium, manganese and zinc from a peak in bottom deposits near the Omo delta to a minimum at the south end of the lake. The decrease is reciprocated by a southward increase in the relative abundance of montmorillonite in the sediments which YURETICH (op. cit.) suggests may be due to the reaction of detrital kaolinite with the alkaline water of the lake.

The influence of the Kerio and Turkwell rivers on sediments is marked by an increase in the soda and potash content, originating from the Precambrian gneisses of the basement complex. Bottom deposits in the Southern Sector are generally lacking in these two constituents supporting the view that currents set up by the prevailing winds tend to sweep discharge from the Turkwell and Kerio rivers northwards into the Central Basin. The Southern Sector appears to derive most sediment from the River Omo probably by sub-surface water currents. The mineralogy of the clay fraction is thus similar to that of the area south of Central Island. Sediments in the Southern Sector are, however, characterised by a relatively high proportion of calcite in the silt fraction associated with ostracod shells.

Discharge from the numerous ephemeral rivers results in a wide variety of sediments in peripheral areas of the lake. Sediments near the east shore are often rich in trace elements derived from metamorphic rocks.

The pattern of vertical distribution of minerals in sediment cores proves that the influence of the River Omo on the lake environment has increased over the past 3,000 years (YURETICH op. cit.). These investigations provide further evidence that the lake is decreasing in size and indicate that there has been an increase in the sediment load of rivers concomitant with a decrease in rainfall over the catchment area. LANGBEIN and SCHUM (1958) have shown that a decrease in effective precipitation to below 750 mm per year can result in an increase in the sediment yield caused mainly by a reduction in vegetation.

The rate of sediment accumulation

The rate of sediment accumulation on the bed of Lake Turkana has been calculated by YURETICH (1976) from the rate at which calcium is removed from the water in the form of calcite. He obtained results ranging from 0.2 mm/year in the southern basin to 2.0 mm/year in the north with a mean of 1.0 mm/year for the whole lake. These calculations are based on known detrital dilutions and a pore water content of 50%.

During the present investigations, sedimentation traps (Fig. 1.22) were used to compare the above estimates with the amount of seston in the lake. Each trap consisted of a 25 cm tube, 5.26 cm in diameter, closed at one end. The tubes were supported on wire frames and attached to a buoyed nylon rope at heights of 1m and 12 m above the lake bed. The arrangment was similar to that described by TUTIN (1955) but the main rope and buoy were fully submerged and a smaller marker buoy on a subsidiary line was used to recover the gear. It is believed that this arrangment minimised movement of the seston traps which might have resulted from wave action. TUTIN (op. cit.) found that tubes suspended from a buoy on the surface gave lower seston sedimentation rates due to such movement. She also showed that straight sided tubes gave the closest correlation with the rate of sediment accumulation on the bed of Lake Windermere calculated from paleomagnetic Pb and stratigraphic marker evidence (reported in PENNINGTON, 1974). The high degree of correlation was thought by PENNINGTON op. cit.) to be due to similarity between the rates of resuspension from this type of tube and from the lake bed.

Sedimentation experiments were carried out at a station 0.5 km north of Central Island with a lake depth of 40 metres. The site provided deep water in a relatively sheltered position. Pairs of sedimentation tubes remained in situ for durations of from 2 weeks to 3 months during the period July to December 1974. Further measurements were made at a more exposed site 1 km north east of Longech spit in 25 m of water for a two week period during December 1974 and January 1975. Tubes were recovered during calm weather and the sediment transferred to aluminium foil in the laboratory prior to drying in a vacuum oven at 70 C. The results (Table 1.5) show that the amount of sediment caught in the tubes varied considerably, possibly as a result of patchiness in the seston (see JONES, 1976). As in TUTIN's studies referred to above, the lower tube invariably contained more material than the upper.

The annual influx of turbid Omo water into the Longech-Central Island region of the lake occurs during early September and the decrease in sedimentation rate between July and September 1974 (Table 1.5) was thus unexpected. Such an anomaly may be the result of resuspension caused by increased water circulation induced both by seasonally stronger winds after September (see Fig. 1.33) and by the input of the River Omo during peak flooding.

The mean value of 12.728 $g/m^2/day$ obtained from the tubes (Table 1.5) is equivalent to a rate of sedimentation on the lake bed of 4.23 mm/year if a density of 2.2 and a pore water of 50% are assumed. This is much higher than the mean rate of 1 mm/year estimated by YURETICH (1974). The difference suggests that material on the lake bed is more liable to resuspension than is the case in the tubes. A relatively high rate of resuspension from the lake bed is a prerequisite for the process by which kaolinite from the Omo input is converted into montmorillonite (YURETICH, _op_. _cit_.).

SHORELINE

The shoreline of Lake Turkana has been studied closely in the course of a survey of the associated fauna and flora, the results of which are presented in Chapter 7. During the course of the survey, over 200 stations were sampled biologically and detailed notes were made at each site on the nature of the environment. Records from these stations were supplemented by observations made during numerous journeys to all parts of the lake, during the four year study period.

Exposure

Many factors contribute to determine the physical nature of the shoreline. The degree of exposure to the effects of wind-induced water movements, both waves and currents, is most important from a biological standpoint. Figure 1.23 illustrates how exposure varies with locality and indicates the direction from which the effects are most strongly felt.

It is clear from Figure 1.23 that shelter is mainly a function of the lack of exposure to the prevailing southeasterly winds. These winds blow most intensely in the Southern Sector of the lake but since fetch is generally longer in the Turkwell and Central Sectors, wave and current action in these areas tends to be as strong as in the south. Northerly winds are relatively uncommon but they may be violent, affecting otherwise sheltered shores.

Ferguson's Gulf is protected from severe wave and current action by Longech Spit. Waves driven by northerly winds are dissipated by a submerged bar at the entrance to the bay and turbulence results from waves created within the gulf.

Substrate

The shoreline of Lake Turkana varies considerably, from flat featureless plains of silt to precipitous coastlines with cliffs rising abruptly out of the water. The nature of the substrate is correspondingly variable (Fig. 1.24). Several important factors influence the distribution of the different categories of substrate, including the degree of exposure to wave action, the presence of bedrock, the slope of the shore, the proximity of water courses, etc. High energy shores where wave action is severe are usually formed of sand, shingle or rock. Low energy shores in sheltered areas are typically muddy.

Certain categories of substrate are not commonly found on the shores of lakes and require special mention.

Black scoriaceous ash is present in areas of the lake where recent volcanic activity has occurred. It has the properties of fine sand. Most of the rocky shores of Lake Turkana are formed of basalts varying considerably in age and in state of erosion. In areas such as the south end of Allia Bay, between Namudak and Kataboi, south of Loielia and south of Loiengalani the shoreline is relatively level but strewn with closely packed, roughly rounded basalt boulders. At the south end of the lake a 5 km stretch of coast is formed by the jagged edge of a series of recent basanatoid lava flows originating from Teliki's volcano. Little erosion has as yet occurred in this area and the substrate consists of contorted masses of deeply fissured rock lava rising steeply from the water to an elevation of up to 6 metres. Similar recent lavas occur on the east coast of South Island, and on the northwest coast of North Island.

Consolidated volcanic ash, resembling sandstone in its physical properties is found in a number of localities and the small islets of Central and South Island are formed entirely of this material. More substantial cliffs of volcanic ash occur on the three main islands but the most striking formations are the cones of Nabuyatom and Agili Agituk on the south shore of the lake. Nabuyatom is a perfect volcanic cone 1.2 km in diameter at the base and 200 m high, with the northern half rising directly from the deep waters of the lake.

Schists and gneisses of the basement complex are confined to a 40 km stretch of precipitous coast, backed by the Loriu range of mountains between Luguruguru and Kalamongin. The surface of these rocks whether in situ on cliff faces or in boulders, is generally relatively smooth.

SHORELINE FEATURES

The build-up of features such as spits, bars and offshore banks is dependent on substrate type, on the energy of the shoreline and on fluctuating lake levels. They are restricted to substrates of sand, ash or gravel which are readily set into motion by water action. The distribution of various features on the shores of Lake Turkana is shown in Figure 1.25.

Spits

The major spits of the western lake shore, Longech, Lolibekai and Meriar are associated with high energy coastlines. Northerly longshore currents scour the lakeward face of the spits and the bottom shelves steadily into deeper water. Sheltered organogenic conditions occur in the shallow water lying in the lee of these promontories. Figure 1.26 illustrates the similarity between the major west shore spits.

In contrast, the principal spits of the east shore including Moite and Koobi Fora (Fig. 1.27) are subject to relatively little wave action but are maintained by currents running along both the inner and outer margins. The currents create extensive submerged and often steep sided bars (see Plates 1.7 and 1.10). Bays formed on the landward side of the spits tend to be deeper and better scoured by currents than those behind spits on the west coast of the lake.

Wave action and longshore currents lead to the formation of minor spits at the mouths of nearly all the small rivers on the lake shore north of Ferguson's Gulf. The tip of the spit often becomes reconnected with the main shoreline, as lake level falls, to create a lagoon separated from the main body of water by a sand bar. Spits do not build up so readily on low energy shores on the east coast and creeks at the mouths of rivers often remain connected to the lake throughout the year.

The delta of the Kerio river is an excellent example of a river mouth situated on a low energy shore. Channels in the delta region of this river are well marked and open at all seasons. They are bounded by levees and dense stands of macrophytes. By contrast the mouth of the Turkwell River a few miles north is exposed to strong southeasterly winds with a considerable fetch. Except during the limited periods when the Turkwell is actually flowing the shore is a continuous line of sandy beaches uninterrupted by branches of the delta.

Sand bars and lagoons

The physical features leading to the development of bars and the lagoons which they enclose are similar to those described for spits. Bar-lagoon systems have frequently developed from spit-gulf formations by a combination of falling water levels and the build-up of material in the entrance to the gulf. The large lagoon at Audache (Fig. 1.3) on the west coast of the lake probably originated as a bay similar to Ferguson's Gulf. Audache lagoon was temporarily reconnected to the lake by a narrow channel during the transgression of the last decade but subsequently became isolated due to falling water levels. The area decreased from over 2 km^2 in 1970 to less than 0.5 km^2 in 1975.

Most of the small river mouth lagoons on the coast north of Ferguson's Gulf are semi-permanent features disturbed only during infrequent interludes when floods breach the sand bars and reconnect them to the lake. After flooding the sand bars are quickly re-established by strong wave action and form a barrier which may rise as much as 2 m above seasonal minimum lake levels.

Much of the open sandy shore of the lake is fringed with a constantly changing series of temporary sand bars, often wave washed, which enclose narrow strips of water. Such temporary lagoons, rarely more than a few metres wide and a few centimetres deep, may be of great biological importance. They shelter a distinctive biota and provide nursery and feeding grounds for fish in an otherwise hostile environment. Conditions tend to be more stable in these temporary pools on the low energy shores than in more exposed situations where the substrate is constantly shifted by wave action.

Shoreline slope

Figure 1.28 illustrates the degree to which the lake bed shelves close inshore in different areas of the lake. As a rule the most steeply shelving shores are situated in the regions of greatest exposure. Shores with massive rock exposures are invariably steep. Finer substrates are maintained at steep angles only by water movement.

Variation in coastal topography

The foregoing account deals with various physical features which are embodied in the shoreline of Lake Turkana. Geographical regions will now be considered separately.

Omo delta to Koobi Fora

The northeast corner of the lake is fringed by flat deltaic plains sporadically cultivated by Dasenach communities. The shoreline is sheltered and gently shelving consisting of broad bays interrupted by infrequent extinct deltaic channels. Forests of dead tree stumps (probably Acacia spp) cover considerable areas extending up to 2 km offshore.

A flat shoreline of sand, muddy sand and mud with occasional areas strewn with pebbles and small stones extends south of the Ethiopian frontier to Ilgimirr (Fig. 1.3). The section also includes two very minor outcrops of rocks on the coast just south of Ilaret. The mouths of rivers flowing into this section, such as the Bani, Ilaret and Tula Bor tend to form shallow, muddy, well vegetated inlets. South of Ilgimirr the coast is interrupted by the basalt slopes of the Kakoi Horst and the shore consists chiefly of boulders interspersed with more massive formations of rock. Between Kakoi and Koobi Fora the shoreline is again flat with a mixture of finer substrates, broken only by the mouth of one significant river.

Koobi Fora to Allia Bay

Koobi Fora spit, with a substrate of coarse sand is a major feature on the east coast. Sandy deposits continue southwards along a 20 km stretch of shore to Allia Bay. The coast faces west-southwest and is moderately exposed both to winds and to the action of northerly currents which lead to the formation of minor spits and bars. The northern limits of Allia Bay are marked by a rocky ridge running to the water's edge. The bay is over 10 km wide and shallow water within the 10 m depth contour extends up to 6 km offshore (Fig. 1.14). Dense emergent stands of macrophytes have become established in muddy areas particularly in sheltered creeks at the mouth of the Bakate river. During periods of low lake level extensive mud banks are exposed at the northern end of the bay (Fig. 1.29). Sandy shores predominate in the central section but to the south, boulders of basalt, at first small and scattered, become larger and more closely packed. Oryx Point at the southern extremity of the bay is a tumbled mass of basalt blocks with deep water close inshore.

Two flat islands are situated in the south of Allia Bay. Skimmer Bank, lying ca 2.5 km offshore consists chiefly of bare gravel resting on a submerged ridge of rock. Low Island lying ca 0.5 km offshore is composed of sand and stones and supports a grassy vegetation.

Allia Bay to Moite

The coast between Allia Bay and Moite, a distance of 40 km, is closely backed by a line of basalt hills, the Jarigole Range. The northern half of this sector consists of rocky outcrops rising precipitously from the lake, interspersed with steeply shelving beaches of shingle. Minor promontories on this coast are generally formed at the mouths of rivers by the deposition of gravel and coarse sand. Nearer Moite the hill slopes become less steep and more continuous stretches of coarse sand and shingle occur on the shore with small scale spits, bars, and lagoons forming as a result of moderate exposure. Huge boulders border the lake at the foot of Mt. Moite. Immediately to the south of Moite Bay, finer sediments including mud and muddy sand have been laid down in the sheltered region protected by the major spit. Moite Spit and adjacent areas of coastline have been formed by the build-up of sediments, chiefly sands and grits, in the delta of the Hadu River.

Moite to Porr

The shore between Moite Spit and Otus Point (Fig. 1.3) backed by low, rolling basaltic hills is relatively flat and featureless with a sandy substrate. Patches of mud are restricted to a few small bays and to occasional minor lagoons. Otus Point is a promontory formed of columnar basalt rising steeply 5 to 6 metres from the surface of the lake. Otus Island, a low outcrop of basalt with stones and gravel supporting a vegetation of stunted Salvadora persica is situated ca 300 m offshore.

South of Otus Point, sandy substrates predominate and with increasing exposure, spit and bar formations feature more prominently. Two deeply enclosed bays, Windy Bay and Sandy Bay, which have formed in the lee of substantial northward projecting spits, are particularly important (Fig. 1.30). The sheltered environment in these has led to the deposition of muddy substrates and to the development of rich organogenic conditions.

The coast between Sandy Bay and Porr faces southwest and the resulting increase in exposure has caused the build-up of a series of bars enclosing small lagoons. The substrate is chiefly sand, but occasional rocky outcrops protect minor bays in which finer deposits accumulate. Porr Point is a low rocky headland with steep cliffs 10-15 m high fully exposed to the rough wave conditions of the southern basin.

Porr to El Molo Bay

From Porr to Khomode (Fig. 1.3) high energy shorelines predominate with coarse sands and fine shingles built up into a series of storm ridges. The coast is interrupted by occasional outcrops of rock. Sand bars and lagoons occur only rarely at the mouths of rivers. Elvato Island, a low bare rocky ridge ca 1 km in extent, is situated in deep water ca 1 km offshore, to the west of the Ballo River.

The long stretch of sandy coast ends with a group of basalt outcrops in the vicinity of Mekeme Island. This island is a low rounded hump of basalt with a sparse vegetation of grass. Between Mekeme Island and El Molo Bay two relatively sheltered bays with extensive areas of mud or muddy sand are separated by a hillside.

El Molo Bay to Nakwe

El Molo Bay, which covers an area of ca 3.5 km^2 is protected by two large basalt islands inhabited by small communities of the El Molo tribe. Fine substrates of mud and muddy sand predominate in the northern sector of the bay and with falling lake levels during 1975 the more northerly island became connected to the mainland by a causeway (Fig. 1.31). The southern margin of the bay near the approach to the open lake is more exposed to wave action and the shore shelves relatively steeply with a mixture of stones and gravel.

South of El Molo Bay the coast becomes more rocky with outcrops of basalt interspersed with more extensive areas of stones and boulders. To the south of Loiengalani the stones at the foot of steep hillsides are often built up into storm ridges by the action of infrequent but violent northerly storms. Fine substrates are uncommon and mud accumulates only in the more sheltered bays such as Loiengalani Bay and the bay to the north of Nakwe. A relatively level sandy coastal plain borders the lake at Nakwe and for a 5 km stretch the shoreline shelves fairly gently with minor sand bars and small lagoons forming on the margin.

Nakwe to Luguruguru

From Nakwe westwards the coast becomes more rugged with a parallel series of olivine basalt cliffs running for at least 10 km down from the mountains of the barrier to meet the lake shore at right angles. The resulting shoreline consists of a series of narrow inlets bounded by low cliffs. The most striking of these inlets, Lotarr, is over 3 km in length with a maximum width of only 250 m.

The stretch of coast west of Lotarr consists of recent volcanics and includes the jagged lava flows originating from Teliki's Volcano and the consolidated ash cones of Nabuyatom and Agili Agituk discussed in the preliminary account of substrate type (see page 19). Beaches of clean sand are located in the two bays between Nabuyatom and the Lotarr inlet.

A more extensive area of sand and fine shingle is situated in the southwest corner of the lake where the shore is separated from nearby mountain ranges by the alluvial plains of Ngangol. Strong wave action creates numerous small bars and lagoons particularly on the more southerly section of this open beachline. Luguruguru Head which forms the northern boundary of the alluvial deposits is a low promontory of basalt with cliffs ca 10-15 m high rising steeply out of the lake.

Luguruguru to Kalamongin

The Loriu Range of mountains rise steeply, often precipitously, from the lake between Luguruguru and Mugurr. As described above, much of the shoreline is formed of schist and gneisses of the basement complex. Wave action is severe and the infrequent beaches which form at the foot of river valleys are chiefly formed of stones and gravel. Extensive stretches of shoreline are formed of large boulders. A limited area of sandy shore with minor spits and bars is situated in the shelter of the promontory formed by the delta fan of the Mugurr River.

From Mugurr to Kalamongin the mountains slope more gently and the lake shore consists of boulders, stones and gravel with only occasional rocky outcrops. Kalamongin Head forms a massive promontory with cliffs dropping precipitously into the lake.

Loelia to Lolibekai

The mountain range terminates in a series of low rounded hills just south of Loelia, and from here to Meriar Point the lake is bounded by open, sandy, windswept plains.

The shore is predominantly sandy with occasional patches of gravel. Deposits of mud accumulate in the infrequent sheltered inlets and in lagoons. Wave action is severe but for substantial stretches the shore shelves very gently and the full force of the surging water does not affect the shallow lake margin. In such areas a grassy swamp vegetation tends to become established. Similar vegetation also occurs in certain shallow lagoons which have developed behind sand bars. Near the northern extremity of Meriar Spit numerous subsidiary spits and bars are continually forming and reforming on the open shore.

Sheltered conditions with a relatively rich vegetation of macrophytes characterise the northward facing shore between Meriar and the Kerio delta. In this region the bottom shelves gently and muddy substrates prevail. Stumps of flooded dum palms (Hyphaene spp) are frequent in this area. Distributaries of the Kerio delta form protected channels open throughout the year. North of the Kerio River, exposure to the southeasterly winds gradually increases and the substrate changes from mud, rich in organic detritus, to sand. Strong wave action builds up deposits at the mouth of the Turkwell River during the non-flood period and the high energy coastline leading up to Lolibekai Point is generally open and featureless.

Lolibekai to Longech

Lolibekai Point is one of the major west coast sand-spits. To the west, in the lee of the spit, is a sheltered bay with deposits of mud and silt. Between Lolibekai and Eliye exposure gradually increases and sandy substrates predominate. A ridge of Pleistocene lake beds joins the lake at Eliye and follows the shoreline north to Audache. The lakeward edge of the ridge has been eroded into a series of crumbling cliffs at a height 20 to 25 m above the water surface. Below the cliffs sand with scattered dum palms slopes down to a narrow exposed beach. The ridge becomes less marked to the north and emerges into an area of low sand dunes in the vicinity of Audache Point. High energy beaches on the point feature a series of sand spits and small lagoons.

The large lagoon at Audache, now separated from the main lake (see page 20), lies between the point and a second ridge based on Pleistocene lake beds which follows the coast north for about 20 km. Near Audache substantial cliffs formed by eroding lake beds are exposed but further north high dunes of mobile sand with scattered dum palms tend to obliterate such features. Sandy substrates predominate on this high energy coast but beds of fragmented sandstone were recently exposed on the foreshore near Audache by falling lake levels and similar formations half buried in sand have been noted near Longech. Approximately 6 km north of Audache a promontory of sandstone protects a small angular bay open to the north. Small temporary lagoon pools, washed frequently by waves, are a common feature through out this stretch of coast. A series of sand hooks forming the outer shoreline of the tip of Longech Spit shelter an extensive system of well vegetated lagoons and inlets. No rivers enter the lake between the Turkwell delta and Ferguson's Gulf. However, a spring of freshwater flows from the foot of the Pleistocene lake beds at Eliye and several patches of freshwater seepage are evident on the shore at the foot of the lake beds north of Audache.

Ferguson's Gulf to Namudak

Ferguson's Gulf, sheltered from the prevailing winds by Longech Spit, has been considered in detail in page 18. Substrates are generally sandy on the east shore which is bounded by sand dunes, and muddy on the west shore. The delta of the Kalakol River extends over a 6 km stretch of shore immediately north of Ferguson's Gulf. Considerable changes were noted in this area during the study period resulting both from falling lake level and a switch in the major river channel. The delta is partly sheltered by Longech Spit and the substrate of the shoreline includes sand, muddy sand and mud. The topography includes a changing pattern of lagoons, inlets and gently shelving open sandy shore with the stumps of partly submerged dum palms.

Namudak to Nariokotomi

From Namudak northwards to Nariokotomi the west shore is open and subject to strong wave actions. Longshore currents result in a relatively steeply shelving profile. Limited shelter is provided by minor spits and bars which form principally at the mouths of the numerous ephemeral rivers. The substrate on the open shore is predominantly sand with occasional concentrations of grits and gravels. Finer deposits tend to accumulate in the mouths of rivers. Harder substrates are confined to a 2 km stretch of coast between Namudak and Kataboi where an area of relatively level foreshore is strewn with stones and boulders of basalt packed close together.

Nariokotomi to Todenyang

Sandy substrates continue north of Nariokotomi but exposure is less severe and the lake shore shelves less steeply. Spits tend to form more readily than in the area further south.

Todenyang to the Omo delta

Shores in the shallow northwest corner of the lake tend to shelve very gently and the coastal topography has changed considerably since 1970. A series of relatively exposed sandy beaches are often breached so that low lying areas adjacent to the lake form shallow well-vegetated lagoons. A more extensive area of grassy marsh lies in the lee of a large flat sand spit situated immediately north of the Todenyang settlement. Low cliffs of siltstone 2-3 m high, with broken wave-washed fragments at the base occur on a 1 km stretch of shore between Todenyang and the frontier. A small patch of the same siltstone forms a nearly level pavement on the shore at the ruined Kenyan frontier post.

The Omo Delta

BUTZER (1971) has described the recent history of the Omo delta in detail, cataloguing changes which have occurred since 1888. Relevant figures from his work are reproduced in the present report (Figs. 1.10-1.12). Two main channels are currently open. Bounded by narrow levees deposited in the period prior to 1961 (Fig. 1.16) they extend 10 to 15 km south into the lake. The shoreline shelves very gradually and extensive areas of shallow water with a rich aquatic vegetation (see page 21) lie in the shelter of numerous bays and channels. Substrates are universally fine.

THE ISLANDS

Twenty permanent islands situated in Lake Turkana are listed in Table 1.6. A number of the inshore islands have been included in the preceding account and the three large volcanic islands, together with their associated islets, are considered below.

North Island

North Island is the smallest of the three major islands. The shoreline includes precipitous cliffs of consolidated tuff jagged flows of recent lava and two beaches of fine ash on the north and west shores. The bottom shelves steeply into deep water. Sulphur jets are still active near the summit.

Central Island

Central Island was described in detail by WORTHINGTON (1932). It is the most complex of the three main islands and includes three crater lakes (Fig. 1.32) referred to as lakes A, B and C by WORTHINGTON (op. cit.). The narrow ridge separating Lake B from the main lake forms the southern rim of a further submerged crater with a maximum depth of 45 m. The present observations show that only minor changes have occurred to these lakes since WORTHINGTON's visit. During the transgressions of 1961-63, crater lake C was reconnected to the main lake. This connection was maintained until early 1972 when falling main lake levels isolated the crater once more.

Sulphur jets noted by WORTHINGTON are still active and, for several days during July 1974, one unusually intense emission of molten sulphur occurred, together with clouds of white smoke, which was clearly visible from the mainland. Due to the large number of crocodiles present, the bathymetry of lakes A and C was not studied, but a sounding of 8 m in the western arm of lake A is similar to a value obtained by WORTHINGTON (op. cit.).

Water in the crater lakes is apparently replenished from the main lake by infiltration. Examination of E R T S photographs showed that the size of these lakes varied with the level of the main lake, indicating that the infiltration rate was relatively high. The biology and water chemistry of these lakes is discussed later.

Figure 1.32 illustrates the bathymetry of the main lake around Central Island, and the positions of the satellite islets. The shoreline is generally steep and rocky. Volcanic sand and gravel interspersed with boulders occur in Crater Bay on the north coast and on the shore near lake C. A more extensive area of sand and gravel is present at the northwest extremity of the island where current action has built up a noticeable spit. Boulders predominate on the more exposed west and south shores, and cliffs of consolidated ash on the north and east shores.

South Island

South Island, the largest of the three islands, was first described in detail by FUCHS (1939). He considered that the island was composed of Upper Pleistocene volcanic rocks based on pre-existing Middle Pleistocene formations. BROWN and CARMICHAEL (1969) later found the rocks to be olivine basalts similar to those of the barrier between the Turkana basin and the Suguta trough.

Beaches of volcanic ash are restricted to relatively small areas on the west coast. Cliffs of consolidated ash are particularly frequent near the north end of the island where several volcanic cones rise steeply from the lake. The east shore is chiefly a jagged mass of relatively recent lavas which extend down to the water's edge. Shores generally shelve very steeply into deep water and wave conditions are often extremely severe in areas exposed to the southeasterly winds.

The island has not been inhabited within living memory but the presence of a feral population of goats together with sherds, middens and fragments of fishnets indicates at least semi-permanent occupation by a community of fishermen-pastoralists.

METEOROLOGY

INTRODUCTION

The East African Meteorological Department have recorded data at Lodwar (altitutde 507 m, grid ref: HBA 897444) and Lokitaung (altitutde 762 m, grid ref: HBH 065713) for many years and the climate of Turkan District is thus well documented. However, it is well known that large bodies of water tend to have a marked local influence on the climate (GEIGER, 1965) and since Lokitaung and Lodwar lie 20 km and 45 km respectively from Lake Turkana, it is probable that their meteorological data are not representative of the actual lake. For this reason a meteorological station was established during the course of the present studies on Longech Spit. The station was located at a distance of 10-15 m from the water's edge on a small subsidiary spit projecting westwards into Ferguson's Gulf (grid ref: HBB 255910). Equipment was installed during the period March-June 1973. Additional data on wind speed and direction was regularly recorded in the log of R V HALCYON during routine cruises to all parts of the lake. From July 1974 to March 1975 a Model M2521 anemometer (see below) was operated at Loiengalani on a site 200 m from the shore, and wind runs were recorded daily by Mr Roberto Rosini of the Italian Volunteer Association.

METHODS

Standard meteorological equipment supplied by Messrs Negretti and Zambra of London was used throughout. Maximum, minimum, wet and dry bulb thermometers were installed in a Model M2811 Stephenson's screen supported at a height of 1.2 m above the ground. Deionised water was used for both the evaporimeter and the wet bulb thermometer. Wind run was measured with a 3 cup Model M2521 thermometer mounted at a height of 2.4 m on a metal pole. Wind direction was observed by means of a weather vane mounted on a pole 6 metres above the ground. Direction was recorded to the nearest octant. Rainfall was measured with a standard 5 inch raingauge Model M2083. A 1 m diameter 'Colorado' evaporation tank was installed during December 1974. The rim of the tank was 10 cm above ground level and lake water was used exclusively.

Data were recorded daily at 10.00 hrs and 16.00 hrs. Most readings were made by locally recruited employees of the Kenya Fisheries Department who had been specially trained for such duties.

RESULTS

Wind

Strong prevailing south easterly winds which are one of the most important climatic features of Lake Turkana were first reported by VANUTELLI and CITERNY (1899). They made 107 observations of wind direction on the north east coast of the lake, 60% of which indicated south easterly or southerly winds. Similar phenomena have been recorded by subsequent visitors to the area including BEADLE (1932) and BUTZER (1971).

The present observations, made over a period of 2½ years provide the first opportunity to detect predictable seasonal patterns in the wind regime. Daily wind runs at Longech, combined to give 10-day means for the period March 1973 to September 1975, are shown in Figure 1.33. The 10-day means varied from 170 km/24 hrs to 475 km/24 hrs with an overall mean of 299.3 km/24 hrs (12.47 km/hr). There were only five days when the run exceeded 60 km/24 hrs and the maximum recorded during a single day was 840 km (equivalent to a mean of 35 km/hr).

No striking seasonal pattern emerges from these results but there is a tendency for the wind run to decrease from a maximum in the early months of the year to a minimum in August or September. This trend was most pronounced in 1974. Interannual variation in wind regime is probably closely connected with major fluctuations in climate affecting a wide geographical area, but the varying pattern of local rainfall is likely to be an important influence.

Daily wind runs at Longech are compared with corresponding data from Loiengalani in Figure 1.34. These results show that winds are considerably stronger at Loiengalani with a mean daily wind run of 760.8 km/24 hrs compared with only 294.8 km/24 hrs at Longech during the 9-week observation period. It is evident from Figure 1.34 that the marked fluctuations in daily wind run at Loiengalani and Longech tend to follow a common pattern with peaks often coinciding.

No regular data are available for the northern part of the lake but records from R V HALYCON indicate that wind speeds were generally lower than elsewhere (Fig. 1.35). BUTZER (1971) provides information on daily wind runs in the Omo delta during the period June-August 1968. He recorded a mean of 163 km/24 hrs which is less than the minimum 10-day mean observed at Longech. It may be concluded from these results that the speed of the prevailing south easterly wind generally decreases from the southern basin northwards up the lake.

Observations on wind direction at Longech are summarised for each month in Figure 1.36. South easterly winds predominate during the morning throughout the study period. Minor differences between the 1974 and 1975 results in the proportion of east and north east winds are probably not significant. Results for afternoon observations (Fig. 1.36) show a much greater variability in wind direction which was particularly marked during 1975. A tendency for south easterly winds to persist in the afternoons is, however, discernable during the period October-March. This coincides with seasonally high wind runs.

Various authors including BEADLE (1932), MODHA (1967) and BUTZER (1971) have commented on a daily rhythm of winds over Lake Turkana, noting a tendency for strong morning winds to be followed by a relatively calm afternoon period. During the present studies detailed records were made by Mrs Lesley Ferguson at the Fisheries Station, Kalokol, of the time at which the wind started, stopped or moderated. These observations were necessarily subjective but since strong winds nearly always arose abruptly, the starting time was usually accurately determined. Results, covering the period March-August 1974 (Fig. 1.37) are in agreement with the findings of earlier workers. On 82.9% of the mornings the wind blew strongly between 09.00 and 12.00 hrs and on 82.7% of the afternoons it was calm between 16.00 and 20.00 hrs. The diurnal pattern of the wind is also shown in Figure 1.38

which indicates that the likelihood of wind blowing strongly increases steadily through the late evening and early morning to reach a peak between 09.00 and 11.00 hrs. Typically, only one windy period occurred each day with a mean duration of 9.88 ± 0.934 h. The time at which winds started to blow varied considerably from early evening to late morning, but over the 5 month period, there was only one record of wind starting between 12.00 and 20.00 hrs. Between March and early May 1974 a relatively high frequency of days on which the wind sprang up at about 08.00 hrs was recorded (Fig. 1.37). This period corresponded with the first major rains of the year. A similar tendency for calm post-dawn conditions was noted during the early rains of 1975.

The factors controlling the diurnal wind pattern are obscure but probably involve the interaction between locally generated thermal air currents and the prevailing Trade Winds. Similar diurnal winds have been described at Lake Chad by HOPSON (1968).

Air temperature

Data were recorded at Longech from March 1973 to September 1975. During this period air temperatures ranged between the extremes of 19.5 °C and 39.9 °C with a mean daily temperature of 29.26°C. Mean maximum and minimum temperatures were 26.03 ± 0.19°C and 32.49 ± 0.15°C.

Seasonal changes over the 2½ year study period are shown in Figure 1.39. Although the regime is remarkably stable, regular annual fluctuations over a very limited range of 2 -3°C in both maximum and minimum temperatures are discernable. The hottest time of the year lay between December and early May with 10-day mean maxima usually lying within the range 32 °C to 33°C. Temperatures started to fall during May and the months of July and August were normally the coolest of the year. Thereafter, temperatures generally increased. Slight inter-annual differences were noted. For example, in 1974 the mean maximum temperature during the cool season fell to only 32.25°C compared with 31.15°C in 1973 and 31.56°C in 1975.

Temperature data for both Lodwar and Lokitaung (HMSO, 1958) show a similar, though more pronounced seasonal pattern with peak values between January and March and the lowest during July and August. A comparison of the present data from the lake shore with records from stations situated well inland, indicates that the large body of water has a stabilising effect on local air temperatures. Thus at Longech mean annual maximum and minimum temperatures differed only by 5.86°C compared with a difference of 12°C (from 23°C - 35°C) at Lodwar, 45 km inland. Records from Kaalom on the River Omo, 20 km north of the lake, collected by the Rev. J SCHWARTZ (pers. comm.) show that conditions are similar to Lodwar with mean maximum and minimum temperatures of 22.8°C and 33.9 °C.

Previous records from Ferguson's Gulf (BEADLE, 1932) and from Central Island (MODHA, 1968) suggest higher maximum temperatures than were observed during the present study. The difference is probably due to the fact that in the earlier observations, thermometers were not housed in Stephenson's screens.

The stabilising effect of lakes on local climate has been discussed by various authors, including GEIGER (1965) and has been shown to be due to the slow rate of heat loss from water compared with land. Measurements of ground temperatures on Central Island (MODHA, 1968) illustrate the rapid rate of heat absorption from the land. The surface temperature of exposed soil rose from 28.5°C at 08.45 hrs to 61.0 °C at 16.00 hrs. This range of temperature is never approached on the surface of the lake.

Rainfall was the climatic factor with the most direct effect on air temperature. A fall in air temperature of up to 8°C was recorded during rainstorms. Temperatures usually rose to normal within 48 hrs of heavy precipitation as illustrated in Figure 1.40. An afternoon change in wind direction at Longech from south easterly to westerly blowing off the land, produced no detectable effect on air temperature.

Relative humidity

Seasonal changes in relative humidity calculated from wet and dry bulb thermometer readings are shown in Figure 1.41. These results indicate that relative humidity was relatively constant with an overall mean from March 1973 to February 1975 of 59.58% + 1.58%. Individual measurements varied from 33% in March 1973 to 90% during rainfall in April 1974.

Humidity levels fluctuated only slightly during the day. The overall mean for observations made in the morning was 58.05% compared with 61.10% for afternoon results. Relative humidity always increased during the build-up to a rainstorm. Values of over 80% were often recorded under such circumstances. Frequently, the storms were abortive and resulted in no precipitation.

Records from Lodwar (HMSO, 1958) show similar variations during the mornings to those of the present study with monthly means ranging from 51% to 54% between January and March rising to above 60% from April to August. The diurnal pattern of humidity change at Lodwar, however, differed strikingly to that noted at Longech. Relative humidity at Lodwar fell to a mean of 36% in the afternoons.

Rainfall

Rainfall data for both the meteorological station at Longech and the Fisheries Station situated 8 km to the west at Kalokol are presented in Table 1.7. Although a similar monthly pattern of precipitation occurred at the two sites there was often considerable variation in the actual volume recorded. These divergences reflect the localised nature of much of the rainfall. Results for the two years (Table 1.7) differ considerably. Thus although significant rainfall was noted in 1973 during the months of September, October and November, none was recorded in the corresponding period of the following year. Marked interannual variation is typical of the more arid regions of the Turkana basin and rainfall data for a number of years must be combined to reveal the true seasonal pattern. Kalokol and Longech 1973 and 1974 records have been pooled to give the monthly means shown in column 5 of Table 1.7. Mean annual rainfall for the two stations thus totals 197.25 mm. Most rain falls during infrequent heavy storms in the course of which precipitation often exceeds 25 mm. The maximum recorded at Longech was 71 mm on 4 July 1975.

Table 1.7 suggests that Lodwar, with an annual mean of 154.9 mm, is somewhat drier than the Ferguson's Gulf area. Records for Todenyang and Ileret, however, indicate a tendency for precipitation to increase towards the northern end of the lake. BUTZER (1971) reports a mean annual rainfall of 360 mm based on 18 years data at Todenyang on the north west shore of the lake and a mean of 308 mm for a 14 year period at Ileret on the north east shore. No data is available for the southern basin of the lake but the sparseness of vegetation in the Loiengalani area suggests lower rainfall than at Ferguson's Gulf, possibly the result of a 'shadowing' effect from Mt Kulal.

THOMPSON (1965) provides detailed maps showing the annual movements of the Inter Tropical Convergence Zone (I T C Z) with its associated belt of rain. Two rainy seasons are likely in areas near the equator, the first after the I T C Z has passed northwards early in the year and the second after its transit southwards. Lake Turkana lies in the path of the I T C Z at a latitutde of ca 3^{o}N and a bimodal seasonal pattern of rainfall distribution might be expected. Results from Ileret (Fig. 1.42) fulfil these expectations. Two peaks of equal amplitude are evident, the first in April, the second in November. Data from Todenyang and Lodwar (Fig. 1.42) differ from Ileret suggesting that the area to the west of the lake might have a different rainfall regime. At both stations a minor peak appears in July and the April peak was much greater than the November-December peak. POTTS (1972) in an examination of East African rainfall data shows that Lake Turkana does in fact lie on a boundary between two rainfall regions. To the east, where the terrain is relatively flat, the typical I T C Z pattern of two equally spaced seasonal rainfall peaks is found. In highland areas to the west, Mt Elgon and the Cherengani Hills interrupt the effects of the I T C Z resulting in peak rainfall during July and August with subsiding peaks in April-May and October (Fig. 1.42). Results from Lodwar and Todenyang indicate that the highland pattern influences climate to the west of Lake Turkana.

Evaporation

GEIGER (1965) has shown that the rate of evaporation from open water is difficult to estimate. The theoretical basis of calculations used by PENMAN (1963) based on Dalton's 'evaporation potential' hypothesis is sound but there are many practical difficulties in measuring the necessary papameters. Estimation of the saturated vapour pressure of the air above water is hampered by complex turbulence in the air above water, caused by waves.

Direct measurement is usually carried out using evaporation tanks floating on the water, a procedure described by FOLLANSBEE (1934). He compared the rate of evaporation from the open water of reservoirs with data from various types of tank and found that floating tanks gave the most accurate results. Wave conditions on Lake Turkana were too severe for floating tanks to be used.

Results from the tank sited on Longech Spit provide an estimate of 5.8 m/year for the evaporation rate. Observations on falling lake levels during the non-flood period (see below) suggest that the actual rate has been considerably overestimated by the tank method. One likely source of error is indicated by the fact that daytime tank temperatures were always about 3^{o}C higher than the temperature of water in adjacent areas of the lake.

An estimate of 3.2 m/year is provided by Piche evaporimeter data (Fig. 1.43). HURST (1957) working on the Nile basin has suggested that a factor of 0.5 should be applied to Piche readings from screens away from water. He believed that where observations are made in close proximity to water (as in the case of the present data) a more realistic estimate is obtained.

Both Piche evaporimeter (Fig. 1.43) and tank data show that although fluctuation in ten-day means occurred, no marked seasonal changes were apparent. Relatively high evaporation rates persisted throughout the year.

Gauge readings from many years show that the level of Lake Turkana tends to fall at a constant rate during the first part of the year. Since all smaller rivers have ceased to flow, input from the River Omo is minimal and rainfall is negligible, the rate of decline is obviously similar to the evaporation rate. Regression equations have been calculated for the linear fall in lake level for a total of 20 separate years between 1945 and 1975 and an overall mean decline of 0.6397 cm/day has been calculated. On this basis a mean evaporation rate of 2.335 m/year ($\pm$ 0.3469 m) is estimated.

It is interesting to note the similarity between the present results and the situation at Lake Chad which also lies in an arid climatic zone. CARMOUZE (1971) estimated an evaporation rate of 2.18 m/year for Lake Chad.

Insolation

Situated 3°N of the equator, Lake Turkana theoretically receives 99.9% of the maximum sunlight possible at any point on the surface of the planet. The angle of declination of the sun at midday reaches a maximum of 36° at the winter solstice on 22 December. This is the shortest day of the year with 11 hrs 55 min of possible sunshine. The sun is directly overhead at noon on 30 March and on 15 September. During the longest day which occurs at the summer solstice a total of 12 hrs 25 min of sunshine is possible. Seasonal variation in the amount of possible insolation is thus relatively small. Smithsonian tables (1961) have been used to quantify the maximum insolation possible at the latitude of Lake Turkana under cloudless conditions. With an atmospheric transmission coefficient of 0.8 an estimate of 668.3 cals/cm^2/day (2797 J/cm^2/day) was obtained.

Direct measurements of isolation made at Lodwar using a Gunn Bellani distillometer (GRIFFITHS, 1971b) give an annual mean of 512 cals/cm^2 /day with a range of monthly means of 456-528 cals/cm^2/day. Comparison of these results with the estimated maximum possible indicates a loss of 28.2% due to cloud cover.

Sunshine records at Lodwar are also available (GRIFFITHS, op. cit.). An overall mean of 8.7 h/day was recorded with monthly values ranging from 8.4 h/day in July to 10.7 h/day in September. These results indicate a 23.4% loss of sunshine due to cloud cover and are thus in close agreement with the insolation data from the same station.

Solar eclipse

A total eclipse of the sun occurred at 16.00 hrs on June 30 1973. During the course of the eclipse, meteorological observations were made every 15 minutes at Longech, situated ca 50 km north east of the path of totality. The most obvious changes accompanying the decrease in insolation (Fig. 1.44) were a drop of 1.7 C in air temperature, a fall in wind velocity from 15.2 km/h to 4.0 km/h and a rise in relative humidity from 60% to 70%. Also noted were a change in wind direction from west to north west and a rise in lake level of 6 mm.

A similar fall in wind speed was noted during the same eclipse in Mauritania by ANDERSON and KEEFER (1973). No significant change in atmospheric pressure was observed either at Lake Turkana (1974) or in Mauritania and the fall in wind speed may have been due to a stabilisation in air temperature. These results support the conclusion that the regular diurnal pattern of wind is associated with changes in air temperatures caused by differential heat loss from water and land.

DISCUSSION

The dry climate of Northern Kenya, Somalia and Eastern Ethiopia is considered by TREWARTHRA (1961) to be the greatest climatic anomaly in Africa. The highlands of Ethiopia and Kenya lie in the path of the onshore tradewinds and should give rise to much wetter conditions than are actually experienced in the region. TREWARTHRA (*op. cit.*) and BUTZER (1971) provide detailed discussions of the factors controlling the climate which are at present not fully understood. GRIFFITHS (1972) quoting TREWARTHRA (*op. cit.*) enumerates the following important influences which may account for the dry conditions:

(i) The divergent character of the northwest and southwest monsoons

(ii) The shallow depth of the southwest monsoon

(iii) The strong meridianal flow in all but the transient seasons

(iv) Stable stratification in the upper atmosphere with a marked decline in moisture content.

In the Lake Turkana area (ii) and (iv) are probably the most impor tantof these factors. GRIFFITHS (*op. cit.*) states that changes in pressure patterns in the upper atmosphere, identified by JOHNSON and MORTH (1960) are responsible for the large variation in rainfall.

The present investigations reveal relatively little seasonal change in any meteorological factor. The stable climate of Lake Turkana is rare among major lakes. Rainfall, which is the most unpredictable feature is also the most disruptive. Heavy rainstorms, often localised and scattered irregularly over the surface of the lake result in a marked fall in air temperature and a sharp rise in relative humidity. They are often accompanied by violent winds and darkness resulting from thick cloud cover. BEADLE (1974) has pointed out that these storms may be very important in the ecology of tropical lakes.

Statistical analysis of data from a 75 day period in 1974 (Table 1.8) reveals no direct correlation between the climatic factors concerned (see also Fig. 1.45). The prediction of meteorological changes is thus difficult and characteristic seasonal patterns only become apparent when several years observations have been averaged. Thus combined monthly temperature data for three stations in the region of the lake (Table 1.9) reveal common climatic trends and form a basis for the recognition of four seasons. Characteristics of each season noted at Longech are as follows:

(i) Season 1 - December (part), January-March:
the hottest time of the year with mean maximum temperatures generally exceeding 33°C; relative humidity at the seasonal minimum; south easterly winds particularly dominant both morning and afternoon; maximum wind runs recorded during this season.

(ii) Season 2 - April-June:
the most unsettled period of the year with the likelihood of rain relatively high in April and May; relative humidity now at a seasonal maximum; wind runs usually high as in previous season but direction more variable; mean maximum temperature 32-33°C.

(iii) Season 3 - July-August:
the coolest period of the year with mean maximum temperature of 31-32°C; relative humidity lower than previous season ; but rain likely in July; wind speed at seasonal minimum; wind direction still more variable than Season 1.

(iv) Season 4 - September-November, December (part):
weather relatively stable; mean maximum temperature 32-33° C; tendency for winds to increase and to blow more constantly from the south east; likelihood of rain increases in November (more particularly on the east side of the lake); relative humidity intermediate between Seasons 3 and 1.

The climates of other major African lakes show more seasonal fluctuation than was observed at Lake Turkana. TALLING (1965) and BEADLE (1974) note seasonal climatic variations on Lake Victoria, lying on the equator, with a bimodal monthly rainfall distribution and changes in wind direction. Such seasonality increases with distance from the equator. JACKSON _et al_ (1963) report marked annual variation in the climate of Lake Malawi (12°S). HOPSON (1968) and CARMOUZE _et al_ (1972) show that on Lake Chad (13°N) the annual rainy season is restricted to a period of 2 or 3 months and the mean monthly maximum temperature may vary by as much as 24°C during the course of a single year.

PHYSICAL AND CHEMICAL LIMNOLOGY

INTRODUCTION

Between November 1972 and March 1975, R V HALCYON made 51 cruises specifically to study plankton and the physical limnology of the lake. Additional information on the water colour change, light penetration, surface temperatures and conductivity was recorded on other cruises, notably those involving echo-surveys of fish populations.

Joint plankton-physical limnology cruises generally took one of the courses shown in Figure 1.46, though time and adverse weather conditions often altered the patterns shown. More frequent observations were made at station H1 situated ca 1.5 km north of Central Island at a lake depth of 80 m (Fig. 1.46). Facilities on board R V HALCYON allowed periods of up to 14 days to be spent 'at sea' although often little stationary work was possible before midday, especially in the windier Southern Sector 'D' (Fig. 1.15).

Methods

Most water temperature readings were taken in plastic-lined, insulated, stainless-steel Nansen-Petersen water-bottles (supplied by Laboratoire Oceanographique, Charlottenlund, Denmark) using a protected mercury and glass thermometer reading from -2^{o} to $+30^{o}$ C with a certified accuracy of 0.05^{o}C. Bottles were lowered on 5/32" stainless steel wire over a recording block suspended from a hydrographic davit on the port side of R V HALCYON. The wire was worked from a subsidiary drum on the Rapp C450W trawl winch. Sampling depths could be checked on the ship's echo sounder. Water collected in the bottles was used for conductivity, pH, dissolved oxygen and ionic analyses.

Conductivity, measured in μS/cm at 25^{o}C (standard temperature of k = $25,^{o}$ WETZEL, 1975), was determined with a Type MC-1 meter (Electronics Instruments Ltd., Hertford, UK) using cells of constants of 1.0 and 0.1

Hydrogen-ion activity was measured with a Model 30 C portable pH meter (Electronics Instruments Ltd.) fitted with a resistance thermometer Model T.30B (EIL) and either an SHDN 33/C (EIL) or a 401/E7 (Pye Ingold, Cambridge, UK) calomel electrode. Both electrodes were capable of discriminating to pH 0.05.

Dissolved oxygen concentrations, expressed as percentage saturation were estimated with a Mackereth-type lead silver electrode (MACKERETH, 1964) in a polythene membrane. The meter was calibrated against standards determined by the Winkler method. Oxygen concentrations in mg O_2/l were found using the nomogram of MORTIMER (1965) modified by WETZEL (1975). A correction for salinity (estimated to be 2.48%) was applied following the procedure of GREEN and CORRITT (1965). The mean atmospheric pressure was taken as 710 mm Hg from initial observations using the ship's barometer.

Underwater light penetration was determined with a submersible selenium-cell photometer, Model 268 WA 300 (G M Mfg, New York, USA), in conjunction with red, green and blue filters (G M Nos. 342, 344, 343 respectively, see Table 1.10).

TABLE 1.10

Filter	Maximum Transmission %		Range nm
G M	Red	85	500-720
G M	Green	65	460-660
G M	Blue	87	300-500

The submersible cell was suspended at a distance of ca 1.5 m from the starboard side of the boat over a fixed horizontal boom situated approximately 2.5 m above the water. The vessel was orientated to ensure that the measurements were always made out of its shadow. Readings with a separate deck cell allowed simultaneous above- and below-water observations to be made.

A plan of the surface-water circulation was compiled from various sources. Observations from boats, land and occasionally from aircraft were used to draft a tentative map. This was supplemented with information from Earth Resources Technology Satellite -1 (ERTS-1) photographs, using spectral bands 5 and 7 (HENSEN et al, 1975).

RESULTS

Water temperature

Seasonal variation with depth

Records from the Station H1 in deep water north of Central Island are plotted as isotherms in Figure 1.47. Readings were taken between ca 13.00 and 15.00 hrs E A T, generally during calm conditions. Initial observations indicate a thermally stratified water body from mid-August to late September with a gradient of 1.9°C in the upper 40 m. Subsequently, surface warming increased the temperature of the superficial layers to 29.4°C and mixing over the whole water column resulted in an increase in bottom temperature from 25.6°C to 26.1°C between December 1972 and March 1973.

Steep gradients were recorded in the upper 20 m from April to August 1973 with a maximum temperature range of 3°C in mid-May. This period was associated with heat loss from the bottom, resulting in temperatures at 80 m decreasing to a minimum of 25.4 °C. From August onwards, the bottom temperatures gradually rose, reaching 26.4°C in November 1973 but thereafter gradually rising to 28.4°C in March 1974. By July 1974, the surface layer was stratifying once more, while the water column below ca 10 m was close to isothermal.

During the 2 year period covered by Figure 1.47 bottom temperatures thus varied by only 1.0°C from 25.4°C to 26.4°C and the immediate subsurface temperature ranged 2.2°C from 27.2°C to 29.4°C.

Daily temperature variation in the open water

The nature of diel fluctuations in water temperature varies seasonally. High air temperatures, a relatively large diel range of air temperature and high winds all contribute to cause widely ranging water temperatures.

The effect of pre-dawn winds on temperatures in the surface layers at Station H1 during November 1972 is shown in Figure 1.48. Falls in temperature ranging from 2.4°C at the surface to 0.9°C at a depth of 10 m were recorded during the night. Very little change occurred in deeper layers. Strong post-dawn winds warmed the surface layers rapidly. Comparable observations made during mid-February, the hottest time of the year, when water temperatures were generally high, are shown in Figure 1.49. Although temperatures in the surface layers fell during the night, the range was generally much less than had been the case in November. Results for August during the coolest part of the year are shown in Figure 1.50. After dark, cooling of the surface layers soon leads to practically isothermal conditions throughout the water column. Marked diurnal fluctuations occurred only in the top 2 or 3 m and at a depth of 5 m a range of only 0.2°C was noted throughout the 24 hour period.

Longitudinal patterns of temperature distribution

Stable climate in the lake basin resulted in relatively constant air temperatures and wind patterns. A narrow range of water temperature both in horizontal and vertical sections reflects this stability, though similar low temperature gradients have been recorded from other rift valley lakes (TALLING, 1965).

Seasonal patterns in longitudinal sections of the lake are illustrated in Figures 1.51 to 1.53.

The most stable conditions of water temperature were noted between June and October when air temperatures were at the seasonal minimum. During this period of 'steady-state' conditions (Fig. 1.51) the Southern Sector was well mixed with a difference between surface and bottom of only 0.5°C in mid-July and 0.3°C in mid-August at the maximum depth of ca 110 m. There was a steady increase in water temperature during August 1974 from below 25°C in the Southern Sector to over 25.5°C in more northerly areas (Fig. 1.51). Temperatures in deeper layers of the Central Sector generally ranged from 25.5 °C to 26°C overlayed by a relatively broad surface zone between 26 C and 26.5°C. Maximum tempertures of over 27°C, during this period, were noted in the surface waters of the Central and, more particularly, the Northern Sectors.

In October 1973 (Fig. 1.52) virtually isothermal conditions, with temperatures between 24.5°C and 25°C were also noted in the Southern Sector, but to the north, on the boundary with the Turkwell Sector, there was a more abrupt rise to over 26°C than was observed in August 1974. Near isothermal conditions were a feature of the southern portion of the Central Sector but in deeper water north of Central Island there was a relatively strong vertical gradient between 25.5-26°C on the bottom and 27.5-28°C on the surface. These horizontal layers extended far into the Northern Sector and although the River Omo was in flood, no cooling influence was detected in the delta region of the lake.

Temperature contours for March 1975, the hottest time of the year, are shown in Figure 1.53. Isothermal conditions are no longer in evidence and vertical gradients of from 1°C to 2°C were recorded throughout the open waters. Figure 1.53 also illustrates a striking north/south gradient with temperatures below 25 °C in the deepest part of the southern basin rising to over 29.5 °C in the far north of the lake. Results for 1973 showed a similar pattern of temperature distribution.

Transverse patterns of temperature distribution

The prevailing south easterly winds blow diagonally across the main axis of the lake and tend to push surface water both towards the west shore and northwards up the lake. The effect of such water movement on temperature distribution is demonstrated by the vertical transects shown in Figures 1.54 to 1.56.

Figure 1.55 shows the situation in the Southern Sector during March 1975, the hottest season of the year when the more usual isothermal conditions typical of this region of the lake have disappeared. Temperature contours slope downwards towards the west indicating a wind induced build-up of warmer water on the west shore. A compensatory movement of colder water from the deeper layers towards the surface on the east shore is also discernable (Fig. 1.55 a and b). Such upwelling is probably characteristic of areas with strong offshore winds and deep water close inshore.

Comparable data for the Central Sector of the lake, collected during various months of the year, are illustrated in Figures 1.56 a to g. Westward tilting isotherms are a constant feature in ech transect. A similar build-up of warmer water is evident in the Northern Sector although this area of the lake is kept highly mixed due to its shallowness and more variable wind regimes (Fig. 1.57).

Inshore temperature effects

Although the southern basin approaches isothermy for much of the year there is evidence of surface warming in the north east corner, north west of El Molo Bay (Fig. 1.3). Warm water is prevented from leaving the basin by the contours of the shoreline east of Porr Point, and builds up as illustrated in Figure 1.58a. In October 1973, temperatures below 10 m were virtually uniform between 25.4° C and 25.45° C but increased steadily to reach 27.3 °C on the surface. A similar pattern was noted off Longech Spit (Fig. 1.58b) during April 1974 with water below 5 m nearly isothermal but with temperatures increasing from 28.6°C to 29.6°C in the top 5 metres.

As a rule, wind-driven water building up to the west tends to obscure any effects of direct warming due to insolation of shallow areas. Sheltered eastern bays, for example Moite Bay, exhibit a gradual temperture rise in the upper 15 to 20 m (Fig. 1.58c). Horizontal circulation patterns are discussed later, but it seems probable that the bays are well mixed, with no distinct thermocline building up.

During periods of unusual calm, however, the shallow bays on the eastern shore of the Northern Sector may exhibit surface warming to a depth of ca 1.5 m illustrated by the profile from Ilaret Bay during March 1975 (Fig. 1.58d).

Dissolved oxygen concentrations

Seasonal changes at Station H1

Dissolved oxygen concetrations close to the bottom in the open water at Station H1 Central Sector ranged from 4.96 to 6.52 mg/l, though they were generally between 5.00 and 5.4 mg/l. This represents saturations of 66 to 86% at depths around 80 m. Concentrations from 6.8 to 8.4 mg/l (92 to 114% saturation) were recorded in the surface water at the same time

These observations were made during the early afternoon and reflect the uniformity of the water in the area. There appears to be little cyclic variation in patterns of dissolved oxygen at Station H1, although supersaturation at the surface was recorded mainly in the presence of algal blooms towards the end of the year, following the movement south of the Omo floodwater. A typical profile from Station H1 is shown in Figure 1.59.

Diel variations in the open water

Results indicate that in water deeper than 15 m there is little diel variation in oxygen concentration. The oxygen present in the open water is mostly introduced by the deep mixing effects of wind-induced currents, which probably persist for some time after the wind has dropped. Thus diel variations tend to be small, even at the surface.

It was observed that respiration by organisms during calm or dark periods reduced surface oxygen concentrations. Thus a mid-afternoon level of 8.3 mg/l (122%) fell to 5.3 mg/l (78%) during a calm night. Such a reduction in dissolved oxygen was not observed to extend into the deeper layers, nor to persist since strong winds usually started before dawn resulting in mixing and increased surface concentrations.

Longitudinal patterns of dissolved oxygen distribution

During calmer periods, an overall picture of increasing oxygen content towards the northern end of the lake is clear (Fig. 1.60). Water in the Southern Sector remains oxygenated right to the bottom, with concentrations not falling below 3.9 mg/l (50%), and surface levels reaching 6.1 mg/l (79%) during mid-afternoon. The tendency for oxygen concentrations to increase northwards up the lake is caused primarily by variations in depth and in circulation due to wind.

Windier conditions early in the year lead to seasonally high oxygen concentrations due to more thorough mixing. Under these conditions levels of 6.15 mg/l (80% saturation) were recorded on the bottom in the deepest area of the lake. The strong wind-induced vertical mixing in the deepest area south of South Island was sufficient to maintain an oxygen gradient of less than 2.0 mg/l over a depth of 100 m.

Results from the Central Sector of the lake show that the effect of windier conditions, as observed in March 1975, was to produce a more even decrease in oxygen concentration with depth (Fig. 1.61). Data for August 1974 (Fig. 1.60) indicated that under calmer conditions dissolved oxygen levels tended to change more rapidly in the top 10 m than in deeper layers.

Figure 1.62 illustrates a selection of dissolved oxygen profiles from stations represented in the longitudinal section (Fig. 1.61a). It is clear that the greatest vertical range of oxygen concentration occurred in the shallow water of the Northern Sector. Supersaturated conditions resulting from intense algal activity were characteristic of this area and wind-induced circulation was strong enough to oxygenate the bottom but not to cause homogeneity.

In the extreme north of the lake the minimum bottom oxygen concentration noted from R V HALCYON was 6.2 mg/l (82% saturation). This level was recorded at mid-afternoon stations and the relatively high concentration may have been due to the mixing effect of strong morning winds. Oxygen profiles from shallow water in the extreme north east of the lake sampled from the Cutter LOROK are shown in Figure 1.63. The observations were made in the afternoon after the wind had veered and decreased from strong southeasterly to light westerly. Oxygen concentrations were uniformly high with a minimum of 8.16 mg/l (144%) close to the bottom.

Inshore oxygen concentrations

Most areas of shallow water on the margins of the open lake were well mixed although on the east coast the prevailing offshore winds were of short fetch. A typical oxygen profile is shown in Figure 1.64 which is based on results from Sibiloth Bay, a sheltered area at the south end of Allia Bay. The samples were taken ca 280 m offshore at noon in a force 4 southeasterly wind. High levels of dissolved oxygen extended throughout the water column. Areas such as Sibiloth Bay are kept well mixed by gross water movements in the open lake creating currents which persist after the wind has dropped. Where shallows are sheltered from such currents, vertical stratification may occur rapidly. In Allia Bay, extensive beds of Potamogeton pectinatus (Linn) occur in water up to 2 m deep. Together with their rich epiphytic communities, these plants cause supersaturation in the top 1.3 m of water during daylight. However, the vegetation hinders wind-induced vertical mixing and creates lowered oxygen concentrations in the deeper layers, even during daylight.

The water at Ferguson's Gulf, though not possessing large stands of macrophytes, is also sheltered from currents persisting in the open lake after cessation of the wind. A long sand spit tends to protect the gulf from the full force of all winds with the exception of those from the north. A shift from windy to calmer conditions generally occurs daily between 12.00 and 16.00 hrs. Figure 1.65 shows changes in the dissolved oxygen regime coinciding with the onset of calm conditions. The gulf is highly productive with dense algal populations which, due to intense photosynthetic activity, cause the water to become supersaturated with oxygen. It was observed that when the gulf was mixed by strong winds the high oxygen content of between 9.55 mg/l (130%) and 9.62 mg/l (135%) was homogeneously distributed throughout the column. Within 30 minutes of the wind dying away, flat calm conditions prevailed (11.30 h) and the oxygen content ranged from 6.35 mg/l (90%) at the bottom to 13.9 mg/l (195%) at the surface. A brief renewal of wind from the southeast at 12.00 hrs caused slight mixing in the surface 30 cm before calm conditions returned, and by 13.00 hrs water deeper than 1.5 m contained 4.0 mg/l (50%). Concurrently, algae in the surface waters had raised the concentrations to over 15 mg/l (greater than 200%). The reduction in oxygen content of the deeper water of the gulf during calm conditions was a regular feature of this productive area.

Discussion on vertical mixing as shown by oxygen and temperature profiles.

The long, narrow basin which is presently occupied by Lake Turkana is situated in a semi-desert area with high atmospheric temperatures. Because of strong prevailing southeast winds and the lake's orientation, water from surface to bottom is maintained permanently in a well-mixed condition even in the deepest areas. As will be demonstrated later, shore topography plays a minor role in determining the degree of shelter from the wind, and may indeed be partly responsible for the very strong winds associated with downslope areas of such features of Mts Kulal, Moite and Jarigole (SCAETTA, 1935).

Wind-driven surface waves directly mix the water-column to a depth approximately equalling half their wave-length (BEADLE, 1974). Boat-work was restricted in extremely windy conditions and impossible when speeds exceeded Beaufort scale 6 (45 km/h). Exceptionally, R V HALCYON steamed in winds to force 8 (64 km/h) with waves estimated to be a height of 4.5 m from trough to crest, and 35 m in length. Work by SMITH and SINCLAIR (1972) on the hydrodynamic effects of wind would suggest that in the southern basin of Lake Turkana, where the average fetch did not exceed 20 km, the depth of the wind-mixed layer does not exceed 12 m during periods of steady force 5 (33 km/h) winds. From their work it is calculated that a steady wind of 33 km/h with a fetch of 20 km and a wavelength of 22 m would generate a depth of significant water transport of 8.2 m, a net transport velocity of 8.8 cm/s and a total transport per metre width of 0.16 m^3/s. Thus considerable volumes of water would be moved downwind from the southern basin of the lake.

In the Central Sector of the lake, records from the meteorological station at Longech indicate a mean wind speed of 12.47 km/h over a 24 month period. If it is assumed that the strong winds blew for only half of this time, then the mean speed would be 24.9 km/h. With an average fetch of ca 35 km at Station H1 such a wind speed is calculated to induce a net transport velocity of ca 7.5 cm/s, a significant water transport to depths of 6.5 m and a total transport of 0.11 m^3/s per metre width. Thus, due to longer fetch, water transport downwind in the Central Sector is probably almost as great as in the windier south. The calculations indicate that during windy conditions about 14.5% of the water in the Southern Sector and 7.9% of the water in the Central Sector is affected directly by wind action and is thus driven north-westwards.

Mixing of the column below the wave-mixed surface layer is effected by secondary currents (see WETZEL, 1975, for a comprehensive description and review). Turbulence occurs between the dynamic superficial layer and deeper, calmer water. In a similar way, friction between the lake bottom and overlying water maintains circulation to the deepest parts (see BEADLE, 1974, for a graphical description of deep water circulation).

Figures 1.51 and 1.53 clearly illustrate the cooling and mixing effect produced by winds in the southern lake. Cooler water is pushed downwind and tends to build up warmer water ahead. As a result, isotherms are tilted downwards to the north and west. Surface waves continue to move water masses downwind for some time after the wind has dropped. The extent to which such water movement effects a temporary increase in lake level under normal conditions on the west shore has not been determined. The pattern of compensatory water movements which lead to a return flow of water from west to east is also not properly understood.

Sudden changes in the wind pattern associated with violent storms have been observed to create a build-up of water downwind before return-currents have had a chance to start. On the west shore in Ferguson's Gulf, during June 1975, the lake level rose by over 30 cm in less than three hours during a storm, as a result of water being blown across the main lake and into the Gulf. Strong southeasterly winds which blow for an average of 9.88 hrs every 24 hrs, probably set up subsurface return-currents persisting for the whole daily cycle. It seems likely that the upwelling of cooler water which was noted on the east shore of the Central and Southern Sector (see above), is part of the return-current system.

The existence of deep water return-currents is supported by sedimentological evidence. YURETICH (1976) has shown that sediments in the Southern Sector are derived chiefly from the River Omo. Surface water movements in the Turkwell Sector occur chiefly in a northwesterly direction and it is probable that a southeasterly return-current, carrying suspended material of Omo origin, flows from the Central Sector through the intervening area to the Southern Sector (Fig. 1.66).

Higher water temperatures in northern areas appear to be a stable feature of the lake. The relatively high levels are probably correlated with lower wind runs and thus less surface cooling, and to permanently depressed isotherms in the area (Fig. 1.67). There is no evidence of isothermal tilting being reversed during calm conditions. A somewhat similar situation has been reported for Lake Tanganyika (COULTER, 1963). This lake, although similar to Lake Turkana in overall shape, is much larger, with a length of ca 650 km, a width of ca 50 km and a maximum depth of ca 1,470 m (BEADLE, 1974). Water below about 100 m in the north basin and 200 m in the south remains permanently anoxic (DEGENS et al, 1973). During the cooler months of June to September, strong southerly winds of up to force 7 (56 km/hr) blow at night, creating a downward tilt of the isotherms to the north, by downwind displacement of surface water. Winds moderate to about force 3 (16 km/hr) at dawn, increasing again in the late afternoon, and are sufficient to maintain tilting for the duration of the cool season. With the onset of calmer, warmer conditions, the hydrodynamic regime alters and the isothermal layers start to oscillate slowly, inclining alternately north and south in the variable winds (COULTER, 1963). During the windy season, a subsurface return-flow is substantial enough to minimise oscillation in surface level which might otherwise occur as a result of the daily wind-induced build-up of surface water at the north end of the lake.

COULTER (op. cit.) suggests that both of the large meromictic lakes of the African rift system, Tanganyika and Malawi, show long term uninodal seiches, initiated by periods of south and southeast winds which later weaken and become more variable, allowing the thermoclines to oscillate during the warm season. ECCLES (1962) recorded large scale oscillations of the thermocline at a particular station in Lake Malawi, but observed no noticeable seiche during the tilting of the isotherms. MORTIMER (1952) describes similar isothermal tilting in the north basin of Lake Windermere after prolonged southerly winds.

Although absolute temperature gradients through 80 m+ at Station H1 in Lake Turkana never exceeded 4.0°C, it must be remembered that a relatively slight temperature gradient in tropical lakes will maintain stratifications comparable to far greater gradients in temperate waters (cf VALLENTYNE, 1957; TALLING, 1969; BEADLE, 1974). The corollary is that a small drop in the surface temperature of a tropical lake may obliterate stratification.

SCHMIDT's formulae for the determination of absolute stability (SCHMIDT, 1915 and 1928) are not applicable to the open water of Lake Turkana, as there is a smooth temperature gradient steepening above ca 10 m rather than a distinct thermocline (see also RUTTNER, 1963; DENNY, 1972; AND WETZEL, 1975, for discussions on density gradients and stability).

Table 1.11 compares Lake Turkana with Esthwaite Water, in England, a fairly shallow, eutrophic, dimictic lake, with a high degree of summer stability. It can be seen that although the temperature differences between surface and bottom of the lakes are very different, the actual density ranges are of similar magnitude.

While nocturnal surface cooling of the open water does not penetrate deeper than ca 30 m (Figs. 1.48 to 1.50), inshore cooling at night sometimes causes temperature inversions in the upper layers (Fig. 1.67). These appear to be short-lived and are probably unimportant in affecting offshore water temperatures. Such is not the case in Lake Albert (TALLING, 1963) where colder inshore water is profile-bound and slides over the sides and bottom of the basin, thus cooling the deeper layers seasonally each year.

Stability of the open-water stratification in Lake Turkana is unlikely to be attributable to solute-dependent density gradients, since salinity and conductivity changes with depth are generally small (see pages 46 to 49 , and TALLING, 1963). Such is not the case with all large tropical lakes. The stratification of Lake Kivu is maintained by salinity gradients despite a temperature increase of 3°C from around 70 to 375 m. In this lake no circulation is apparent below 70 m (DAMAS, 1937, 1938) constrasting sharply with Lake Tanganyika which, though permanently anoxic below 100 to 200 m, is chemically well-mixed to the bottom (DEGENS et al, 1973). DEGENS et al (op. cit.) suggest that the deep-water gradients in Lake Kivu are due to jets of warm, saline water issuing from cones in the north basin bed. No evidence of similar phenomena was recorded in Lake Turkana, despite volcanic activity on two of the main islands, and irregularities in the lake bottom topography (see pages 25 to 27).

The influence of winds on the stratification of other large rift valley Lakes is discussed in works by BEADLE (1974) and TALLING (1969). DAMAS (1937) suggests that Lake Edward overturns irregularly, about once a year, while BEADLE (1932, 1936) reports the water to be anoxic below ca 60 m most of the time. BEADLE (1974) referring to TALLING (1963) states that the winds impinging on the surface of Lake Albert are stronger than those over Lake Edward and that during August they create well-mixed water with near-homogeneous thermal and chemical properties. However, they are neither as strong nor as persistent as those over Lake Turkana, and it appears that much of the cooler, deeper water originates from the nocturnal cooling of the shallows referred to above.

Water Conductivity

Introduction

Investigations in the mixing of water bodies differing markedly in salinity are greatly facilitated by the use of a conductivity meter which enables the pattern of salinity distribution to be plotted rapidly. In temperate regions the conductivity of water in inflowing rivers is usually too similar to that of the main body of the lake for their approach to be practicable and studies are confined chiefly to the estuarine environment. Conductivity measurements have been used, however, to investigate the influx of polluted water of relatively high conductivity into the Great Lakes of North America (MODIN and BEETON, 1970; AHMSBROK and RAGOLZKIE, 1970).

Conditions are usually more favourable for this method of investigation in enclosed lake basins of hot arid areas where high rates of evaporation result in an elevation of lake conductivity well above that of inflowing rivers. Thus HOPSON (1969) and CARMOUZE *et al* (1972) used surface conductivity measurements to demonstrate the surface circulation of Lake Chad, and SERRUYA (1974) traced the dispersion of water from the River Jordan into Lake Kinneret by a combination of vertical profiles and surface conductivity maps.

An ideal situation was found in Lake Turkana where the conductivity greatly exceeded that of the inflowing rivers. Surface water conductivity measurements were made during hydrographic and other lakewide cruises at 2.7 km (15 minute) intervals. A typical survey pattern is shown in Figure 8.68 for cruise numbers 224 and 225 from which conductivity maps for November 1974 was constructed. Cruises often took several days to complete but it appears from the results that the water movement was sufficiently slow to make little difference to the overall pattern of distribution.

In addition to the surface observations, vertical profiles were constructed from conductivity measurements made on water collected from different depths at routine hydrographic sites.

Results of the surface conductivity surveys are shown in Figure 1.68 which clearly show seasonal changes in distribution patterns.

Seasonal variations in lakewide surface water conductivity

June 1974 (Fig. 1.68a)

These observations were made at the commencement of the annual flood period when the lake level had fallen to the seasonal low.

The River Omo, with a conductivity of about 80 µS/cm, had recently started to discharge, resulting in a marked salinity gradient in the northwest corner of the lake with conductivities below 2000 µS/cm in the vicinity of the delta. The area affected by the influx of Omo flood water did not extend more than 40 km south of the Omo delta and conductivities over most of the Northern Sector varied from 3400 to 3500 µS/cm. Slightly higher conductivities were recorded in the Central Sector and on the west shore north of Ferguson's Gulf a pocket of water with a conductivity of over 3700 µS/cm was detected. Apart from this small isolated area the highest conductivities, with readings between 3600 and 3700 µS/cm were observed in the Turkwell Sector.

August 1974 (Fig. 1.68b)

By now the River Omo had been in flood for nearly two months and the level of the lake had been rising since early July indicating that input exceeded evaporation. Figure 1.68 shows that, although the area influenced by inflowing water had increased considerably, it was still confined to the west side of the lake in the Northern Sector. Thus, although conductivities as low as 1400 µS/cm were recorded near the Dierhale branch of the Omo delta, values above 3500 µS/cm were obtained near the east shore at Ileret, only 10 km to the southeast.

A slight east-west gradient was also present in the Central Sector where a broad tongue of water of 3400 µS/cm extended south east into the area round Central Island. This tongue represents the limits of the influence of the inflowing Omo flood water on the surface during the sampling period.

South of Central Island conductivities gradually increased and as in June much of the Turkwell and Southern Sectors lay within the 3600 µS/cm contour.

September 1974 (Fig. 1.68c)

The lake level had now been rising for over three months and a considerable volume of water had entered the lake. The presence of this water was indicated by an extensive brown sediment plume which had spread as far south as Central Island. The overall pattern of salinity distribution shown in Figure 1.68 was similar to that observed in August, but the gradients were steeper. Conductivities adjacent to the Omo delta in the northwest corner of the lake had fallen to below 200 µS/cm and a strong west to east conductivity gradient was once again a striking feature in the Northern Sector with conductivities between 3300 and 3400 µS/cm persisting near the northeast shore as far north as Ileret.

Conductivities had fallen below 3300 µS/cm over much of the Central Sector but a pocket of high conductivity water noted near the west shore north of Ferguson's Gulf in June 1974, was again present. This inshore area was not included in the August 1974 survey. Figure 1.68 indicates that the main influx of floodwater in the Central Sector tends to occur in a southeasterly direction.

In the Turkwell and Southern Sectors conductivities had fallen slightly and now lay mainly below 3600 µS/cm but the pattern of conductivity distribution had changed little since the previous month. As in August, lower conductivities were recorded in the area south and east of South Island and higher conductivities were observed near the west shore south of Meriar Point.

November 1974 (Fig. 1.68d)

The discharge from the River Omo was now greatly reduced with the cessation of annual flooding. The pattern of surface conductivity distribution in the Northern Sector had changed considerably since September. The most striking feature was a reversal in the east to west salinity gradient resulting from northward movement of a wedge of relatively high conductivity water up to the west shore. As a result the area of lowest salinity, with conductivities between 1800 and 1900 µS/cm, now lay near the east shore in the Ileret area.

In the Central Sector the pattern of surface conductivity had also changed with lower conductivity east of North Island spreading southwest across the Sector towards Central Island. Higher conductivities were also recorded north of Ferguson's Gulf.

Surface conductivities in the Turkwell and Southern Sectors had generally increased since September but values of under 3500 µS/cm were still recorded near the Turkwell delta and in the area between South Island and Loiengalani.

March 1975 (Fig. 1.68e)

By now the lake level had been falling for four months and as a result of greatly diminished inflow from the River Omo, conductivities in the delta area had increased to over 3200 µS/cm. Surface conductivities over the lake as a whole were relatively uniform, although values tended to be generally higher in the south. Isolated pockets of water with high conductivities, previously seen in June and September, were noted near the west shore north of Ferguson's Gulf and south of Kerio Bay.

The proportion of the surface covered with water of higher conductivity in the Turkwell and Southern Sectors was still higher than in the Northern or Central Sectors and thus the gradient of increasing conductivity from north to south persisted throughout the year. However, it seems likely that further stabilisation occurs between March and June before the Omo River starts to flood.

Conductivity profiles from lakewide observations

Vertical conductivity profiles have been constructed from data collected at routine sampling stations during hydrographic cruises.

August 1974

Figure 1.69 illustrates lakewide variations in the form of vertical profiles from August 1974. Thus at the most northerly station there was a difference of 1700 µS/cm between the comparatively fresh water on the surface and the more saline water on the bottom. In contrst, over most of the lake away from the influence of the inflowing Omo river water, conductivity readings varied only slightly with depth.

Data from August 1974 have been used to prepare a vertical north to south section of the lake (Fig. 1.69b). This section on which isoconductivity contours have been plotted reveals important features which were not apparent on the surface conductivity map.

The relatively fresh inflowing water penetrated southwards over a residual pocket with an appreciably higher conductivity of over 3600 µS/cm, situated north of North Island (Fig. 1.69). Vertical salinity gradients were less marked in the Central Sector of the lake but a subsurface movement in the direction of Central Island of slightly fresher water with conductivities between 3300 and 3400 µS/cm is indicated by the contours in Figure 1.69. Comparable surface conductivities were not recorded further south than 12 km south of North Island (Fig. 1.69). The tongue of low conductivity water was sandwiched between water of 3500-3600 µS/cm situated both on the surface and near the bottom. It seems likely that the superficial layer had been blown over the tongue of lower salinity water by the prevailing southeasterly wind. The depth range of the superficial layer corresponds closely with the depth of significant water transport estimated for the Central Sector of the lake (see above p 41).

The results for August 1974 suggest that lower conductivity water from the north has just started to affect the Turkwell Sector but the Southern Sector remained unaffected. The vertical section in Figure 1.69 shows that a layer of more saline water over 3700 µS/cm was present on the bottom of the Southern Sector. It is probable that this deep layer extended westwards into shallow water and is continguous with the patch of higher conductivity surface water situated near the western shore of the southern basin at this time (Fig. 1.69).

October 1973

No lakewide hydrographic cruises were made during October 1974 but data is available for October 1973. These observations which are illustrated in Figure 1.70 indicate that flooding from the River Omo during 1973 followed a pattern similar to that demonstrated for August 1974 (see above).

Results from October 1973 show that, with the flood season now approaching its final phase, the river water had influenced the whole of the Northern Sector. Vertical profiles at all stations within this sector showed a marked increase in conductivity with depth. This was most obvious near the west coast where a surface conductivity of 1250 µS/cm was recorded compared with 3100 µS/cm on the bottom at a depth of 6 m.

Outside the Northern Sector vertical profiles showed that the conductivity varied only slightly with depth and that the gradients were even smaller than those seen during September 1974.

The vertical section (Fig. 1.70) shows that pockets of high conductivity in the Northern Sector, observed in August 1974, were not present in October 1973. The regular pattern of isoconductivity contours extending well into the Central Sector reinforces previous evidence which indicates that the southward penetration of floodwaters increases in momentum from the bottom to the surface. The tongue of subsurface water of 3300-3400 S/cm overlain by more saline water, which was a notable feature north of Central Island during August 1974, was also present in October 1973 but was situated further south.

Conductivities over most of the Southern Sector were similar and lay within the 3600 S/cm contour. Readings were generally slightly lower than during August 1974. Figure 1.70 provides more evidence of wind-blown surface currents; the section at the southern end of the lake indicates northward movement of water with conductivity level between 3500 and 3600 µS/cm over more saline subsurface water.

December 1974

The observations made in December 1974 were limited to the Northern and Central Sectors of the lake. By this time the Omo flood season had finished and conductivities in the Northern Sector had risen considerably, particularly in the delta region where the lowest reading was now 2700 µS/cm (Fig. 1.71). Vertical conductivity gradients, with higher conductivities recorded near the bottom, were still present but in the Northern Sector they were much less marked than those seen in the flood season.

The vertical section for December 1974)(Fig. 1.71) indicates that, in contrast with the Northern Sector, conductivities in the Central Sector had decreased since the flood season due to a marked expansion of water within the 3300 µS/cm contour. This body of water now occupied much of the upper 50 metres of the water column in the area north of Central Island. The subsurface tongue of water with conductivity levels between 3100 and 3200 µS/cm in the area south of North Island is a feature of interest. It seems likely that, as in previous months, this is the result of wind-induced surface currents causing more saline water from the south to be blown over the adjacent mass of water lying to the north.

March 1975

Vertical conductivity profiles for March 1974 (Fig. 1.72) support the evidence from surface observations (Fig. 1.68c) which shows that, compared with the flood season, the lakewide variation of conductivity levels was minimal. Conductivities at the northern extremity of the lake had now risen to over 3400 µS/cm and at the station just south of the Omo delta there was an increase of only 80 µS/cm between the surface and the bottom.

The northward tilt of the isoconductivity lines in the Northern and Central Sectors, clearly shown in the vertical lake section (Fig. 1.72) probably indicates the continued effect of the northerly wind-induced surface currents. Deep areas of the lake of the Central Sector, below the 60 m level, remained markedly similar throughout the period covered by the vertical sampling programme with conductivities not fluctuating outside the 3500-3700 μS/cm range.

The Turkwell and Southern Sectors contained water with conductivity levels mainly between 3500-3700 μS/cm with an area of relatively low conductivities persisting between South Island and Loiengalani. To the north of this region higher conductivity water above 3600 μS/cm persists on the surface up to a line between the Turkwell delta and Sandy Bay. The two areas below 3600 μS/cm are connected by a midwater layer of lower conductivity rates in the Turkwell and Southern Sectors shown on the vertical profile. This subsurface connection was not clearly visible in the previous months.

Transverse vertical profiles

Conductivity profiles from east-west transects of the Central Sector have been used to construct the transverse sections of the lake shown in Figure 1.73. The results from October 1974 are in general agreement with the surface and the longitudinal profiles discussed above. The spread of relatively low conductivity water near the west shore is clearly demonstrated in Figure 1.68c. A tendency for higher conductivity water to spread westwards in the surface over deeper less saline water is also evident. This situation probably results from wind-induced surface currents moving in a northeasterly direction. Similar effects have been noted above in the discussion of longitudinal lake sections.

The dispersion of water from the Kerio and Turkwell Rivers

The dispersal pattern of water flowing into the lake from the Turkwell and Kerio Rivers is illustrated by a map of surface conductivities (Fig. 1.74) for June 1972. Evidence from this map, combined with subsequent observations on the movement of sediment plumes in the area, suggests that the strong prevailing southeasterly winds set up currents which carry the floodwaters northward past Lolibekai Point into the southern part of the Central Sector. There appears to be little lateral movement of water and more easterly areas in the Turkwell Sector remain relatively unaffected by heavy flooding. Stratigraphical evidence supports these observations. YURETICH (1976) found that although the input of the Turkwell and Kerio Rivers is characterstically high in soda and potash, sediments in the Southern Sector contain disproportionally low fractions of these compounds.

Conductivity measurements in Ferguson's Gulf

The characteristic pattern of surface conductivities in the Ferguson's Gulf area, based on data collected in April 1975, is shown in Figure 1.75. These data support the visual evidence of the distribution of water bodies in the area discussed above (see Plate 1.2). It is evident that within the Gulf, water tends to circulate in a clockwise direction. Relatively low conductivity water enters the Gulf from the open lake to the northeast and high conductivity water, dark green in colour due to high algal concentrations, flows northwards out of the Gulf as a discrete current close inshore. COLE (1968) suggested that Ferguson's Gulf would have a higher salinity than the open water because of its similarity to the Gulf of Karabugas in the Caspian Sea. These relatively large and shallow inshore areas which are almost cut off from the main basin have higher evaporation rates than the open water and consequently have higher salinities. It is interesting to note that higher salinity water is carried out of both these Gulfs into the main lake. In Lake Turkana the passage of this higher conductivity water many kilometres up the west shore is clearly visible from the water colour and may be the source of the pocket of high conductivity water which persists close to the west shore of the Central Sector, noted above.

Seasonal changes in conductivity at Station H1

During the period January 1974 to February 1975, monthly vertical conductivity profiles were constructed from samples taken at Station H1. Isoconductivity contours have been fitted to this series of profiles to demonstrate seasonal changes in vertical salinity distribution (Fig. 1.76). The relatively rapid increases which took place at the beginning of the year are correlated with a seasonal increase in the wind speed which led to a rise in the volume of high conductivity water being blown into the area from the south. Conductivities tended to fall in the remaining months of the year chiefly as a result of the influx of floodwaters from the Omo. With the termination of the annual flood season in November a general rise in conductivity was noted.

Discussion

The evidence presented above provides a clear picture of how the major freshwater inflows become dissipated in the main body of the lake. The dispersal patterns observed were in most cases attributable to the effects of wind-driven currents generated by the strong prevailing southeasterly winds.

It is likely that the sequence of events, noted during the present investigations and summarised in the following paragraph, is repeated as a regular cycle each year. Marked interannual variations are likely to occur since rainfall, and hence river discharge, varies considerably.

During June when the River Omo commences flooding, low salinities are confined to the northeast corner of the lake. Elsewhere, conductivity levels are relatively uniform at about 3500 μS/cm, but tend to increase slightly to the south. In August there is a slight reduction in salinity in the Central Sector and by September the flooding has reduced the conductivity of the water in the Turkwell and Southern Sectors. This fall is of short duration in the Turkwell and Southern Sectors and by November the conductivity of the water has increased to the pre-September levels. During December similar increases occur in the Central Sector and by March conductivity levels are relatively uniform throughout the lake although a slight increase from north to south persists.

Lake Circulation

The pattern of circulation in Lake Turkana has been determined from a variety of evidence, both direct and indirect. Much of this evidence relating to temperature and oxygen profiles and to conductivity measurements has already been discussed in the preceding pages.

It is concluded that the strong prevailing southeasterly winds are the principal cause of water movement. The wind-induced surface currents are restricted to the top 6 or 7 m but they are strong enough to create subsurface counter-currents which in turn cause mixing throughout the water column. The effectiveness of this mixing is demonstrated by the absence of a deep water thermocline and of an anoxic hypolimnion. In several cases it has been possible to trace subsurface counter-currents from the pattern of conductivity distribution demonstrated by results from the Central Sector of the lake during August 1974 (Fig. 1.69).

Satellite photographs supplied by E R T S provide further information on the annual influx of River Omo water and of its subsequent dispersal in the lake. Sediment plumes formed by turbid river water are clearly visible on the photographs. Unfortunately, the satellite camera was out of action in 1974 when most of the limnological data presented here was recorded, but the seasonal changes in the outline and the extent of the discoloured areas on the 1972 and 1975 photographs (Plates 1.12 a-g) closely parallel changes in the pattern of surface conductivity described above (Fig. 1.68 a-g). This also suggests that a similar course of events is followed each year.

Systematic observations, mainly from echo-survey cruises, on the seasonal spread of highly coloured water from the River Omo were used to supplement information from E R T S photographs. Maps showing the distribution of this water are presented in Figure 1.77. In the initial stages of the flood season the brown/green water interface was clearly defined and showed very similar patterns to those seen on the satellite photographs in Plate 1.12.

As the flood season progressed, the interface became less distinct and subtle changes in water colour were observed from the research vessel which were not evident from the satellite photographs. Figure 1.77a shows the extent of the different colours of water observed from R V HALCYON during September 1974. Most features are similar to those illustrated by the satellite photographs (Plate 1.12) and the surface conductivity map (Fig. 1.68). However, it is clear that the sediment plume, although somewhat dilute, extended southwards across the Central Sector of the region of Central Island. The distribution of brown water in November 1974 is shown in Figure 1.77b. It is evident that the sediment plume had by then extended down the east shore to the region of Koobi Fora. The results agree closely with evidence provided by the conductivity map for November 1974 which demonstrates a reversal in the current pattern in the Northern Sector following the flood period.

The probable circulation pattern of Lake Turkana, based on all the available data is shown in Figure 1.78. Surface water tends to move in a northwesterly direction and this movement is compensated for by a reverse flow of deeper water to the southeast. Exceptional circumstances prevail during the flood season when a southerly movement of low salinity water down the west shore of the Northern Sector is set up by the inflowing water. The circulation reverts to the normal lakewide pattern in the Northern Sector when the river discharge subsides in November.

In conclusion, it can be stated that although the strong southeasterly winds are the 'prime movers' of the lake's limnology, the main agent of change is the inflow of freshwater from the River Omo.

Underwater light penetration

Introduction

Routine measurements of light penetration were made at hydrographic sites. They provided supplementary information for the interpretation of physical and biotic phenomena and, at the same time, contributed to the evidence on which overall conclusions about the lake's characteristics have been based.

The first part of this section deals with results obtained with the GM 268 WA 300 submersible photometer, used with a pearl diffuser disc. Extinction coefficients (ϵ) in ln units/m were calculated for each site employing both graphical and mathematical methods (see REID _et al_, 1975).

The formula used was $\epsilon = \frac{1}{d} \log n \frac{I_1}{I_2}$ where I_1 is the light intensity at depth 1, I is the light intensity at depth 2, and d the difference in metres between depths 1 and 2. Nomenclature follows that of TALLING _et al_ (1973). Sites used to plot information specifically for the comparison of different lake sectors are shown in Figure 1.79.

The lower limit of the trophogenic zone of a water body is usually considered to be the depth at which 1% of the non-filtered light incident at the surface, is recorded by the photocell. Such a definition is used here.

Seasonal changes in light penetration at Station H1

Regular observations of light penetration were made at Station H1 (Station 6, Fig. 1.79), during the period October 1972 to March 1975. A marked seasonality is evident (Fig. 1.80). The extinction coefficient was less than 1.0 for most of the year, and thus the lower limit of the trophogenic zone was deeper than 5 m. During September, with the sudden influx of turbid water into the area, the value of ϵ increased considerably and the trophogenic zone narrowed to less than 2.5 m. Water clarity increased during the following two months, and by December, values of less than 1.0 were again recorded.

Southwards, the seasonal influx of turbid water occurred progressively later and became less marked. Minimal values of ϵ were recorded as late as March at Station 10 (Fig. 1.79) in the vicinity of South Island, some 5 months after the Omo had ceased flooding.

Values of extinction coefficients recorded for Ferguson's Gulf ranged from 7.8 to 15, with 1% light penetration from 60 to 45 cm. These results were obtained from measurements at times of calm, soon after cessation of the strong southeast winds. The high values are due principally to attenuation by dense algal standing crops (up to 390 µg chlorophyll _a_/l).

Variation of light penetration with locality

The relationship between ϵ and distance from the north end of the lake, (i.e. from the River Omo delta) is illustrated by curves (i) and (ii) in Figure 1.81. Both curves follow a similar pattern with high ϵ values recorded from the turbid waters of the North Sector, falling to low values in the south. Maximum values of ϵ at each station were obtained when the seasonal influx of turbid floodwater was at a peak, and minimum values coincided with the period during the non-flood season when the water contained least suspended material.

Seasonal variations in the value of ϵ are much greater at stations in the Northern and Central Sectors than in the south. This is due to the annual incursion of sediment plumes of Omo origin which do not greatly influence more southerly sectors.

Table 1.12

Station (Fig. 1.46)	Distance from River Omo (km)	1% response depth (m) Min.	Max.
3	25	0.5	3.7
6	105	2.11	9.8
8	162	4.0	8.5
11	230	10.25	13.0

Table 1.12 gives data for 1% limits from selected sites along the longitudinal axis of the lake. These show that the depth of the tropogenic zone increases considerably from north to south, but that seasonal variations are greater in the more northerly sectors.

Plots of light penetration, expressed as a percentage of the incident surface light, against depth, for Stations 1-11 are shown in Figures 1.82 and 1.83, to illustrate further the transmission and attenuation of light by the water at times of maximum and minimum turbidity. The overall picture is one of greater transparency and higher transmission of light with increasing distance from the River Omo mouth.

Transmission of light at various wavelengths

By fitting coloured filters to the submersible photocell, attenuation of light at various wavelengths could be determined.

Curves are shown (Fig. 1.84) for site 3, in the Northern Sector during flood (i) and non-flood (ii) seasons. In the flood season, red light penetrated most strongly ($\epsilon = 2.26$) and blue light least ($\epsilon = 4.95$) with the curve for green light being intermediate. In the non-flood season, light transmission had risen in all three colours but the increase was greatest in the case of green light, with an extinction coefficient ($\epsilon = 1.80$) approaching that of red light ($\epsilon = 1.69$).

Comparable results for the Central Sector are shown in Figure 1.85. The situation during the flood season is similar to that of the Northern Sector. Penetration is again greatest in the red waveband ($\epsilon = 1.45$) and least in the blue ($\epsilon = 3.81$). In the non-flood season, the shift in absorption towards the green wavelength was more marked, with values of $\epsilon = 1.21$ (green), 1.29 (red) and 2.35 (blue) being recorded.

Data from the Southern Sector were obtained during March 1975, when effects of the previous flood season were still in evidence (Fig. 1.86). The tendency for increased penetration of green light is more marked than in the Central Sector during the non-flood season. Extinction coefficient values of 0.52 (green) 0.64 (red) and 0.96 (blue) were recorded.

Discussion

Limitations of the method and equipment used

The responses of the coloured filter discs used in conjunction with the submersible photometer permitted observations to be made on three broad wavebands. This arrangement was adequate for comparisons to be drawn between stations and seasons on Lake Turkana, and with previous studies from other localities. However, coloured filter discs permit only general trends to be seen, and spectroradiographic measurements are necessary if narrow attenuation peaks are to be accurately described and compared (see TALLING *et al*, 1973).

The determination of extinction midpoints by the methods used in the present investigations is not considered very reliable due to the relatively wide transmission spectra of the filter discs. In addition, accurate results cannot be expected where extinction coefficients exceed 10, due to the short depth-ranges involved in turbid waters, coupled with movements of the boat and surface waves.

Whenever possible, photometer readings from below the top 2-3m were used to construct curves for the determination of ϵ. In this way, misleading values from heterogeneously distributed phytoplanktons and from photocell saturation near the surface were avoided. However, in most cases, the log-normal intensity/depth plot yielded a satisfactory line relationship with the shallower values included. Repeatability of results over a period of days at one particular site during the non-flood season was good.

The use of the 1% light penetration depth (99% attenuation point) is used in the present account to facilitate comparisons between waters and stations, and it not necessarily intended to indicate absolute 'compensation' depth, where the ratio oxygen consumption : production is unity.

The present results show that extinction coefficients tend to decrease progressively from the mouth of the River Omo southwards, throughout the lake. Clearly, the sediment load from the principal inflow causes highly turbid conditions.

While Figure 1.81, curves (i) and (ii) indicates the extreme annual maxima and minima of ϵ at stations down the mid-line of the lake, these values do not occur simultaneously at all sites. Thus, Omo flood water affects transparency in the Northern Sector mainly during August and September, but in the Central Sector, at Station H1, the influence is greatest from mid-September to mid-December. Further south, the effects are even more delayed and weaker, occurring from October to February at Station 7, south of Central Island, and as late as March at Station 10 in the extreme south.

Conductivity data and E R T S photographs show how, during the flood period, the main influx of water is restricted to the west shore of the northern basin. The resulting east-west salinity gradients are accompanied by marked transparency changes, with cleaner water present near the east shore. The photometry results based on the longitudinal series of stations fail to show these local variations except in the case of Stations 2 and 3 (Fig. 1.81). Although Station 2 is close to the delta, it lies further east than Station 3. As a result of the transverse transparency gradients, peak extinction coefficients may occur at Station 3 earlier than at Station 2 - as was the case in September 1975. Data from September 1975 also indicate the close relationship between lowered surface conductivities and turbid water, especially during the earlier stages of the Omo flood (Fig. 1.87).

Seasonal reduction in light penetration associated with the influx of turbid waters has been demonstrated for Station H1 in the Central Sector (Fig. 1.80). Surface conductivities at times of maximum light penetration were generally between 3,500 and 3,610 µS/cm, but fell during the period of increased turbidity, mid-September to mid-December, to below 3,300 µS/cm.

The wavelength of light which penetrates furthest is dependent upon solutes and suspensions present. Photosynthetically available radiation lies between 400 and 700 mµ and typically, different wavelengths are attenuated or transmitted in different lakes. Distilled water transmits light of ca 460 mµ (blue) most and 680 mµ (red) least. Crater Lake, Oregon, which has been described as an 'analogue of distilled water' by SMITH and TYLER (1967), transmits blue light strongly. Such properties are exceptional and in most lakes green light, ca 520 mµ istransmitted most strongly.

In lakes with a high organic content, very little light of wavelengths shorter than 600 mµ penetrates to depths greater than 1 m and red light penetrates furthest. High red light penetration is also typical of highly turbid waters where inorganic suspended solids result in elevated extinction rates.

Areas of high turbidity in Lake Turkana absorb blue light most strongly, while ϵ min is generally in the red region (Fig. 1.84). Clearler areas, eg Station 10 (Fig. 1.79), transmit green light most strongly. This pattern is paralleled by Lake Powell, in an arid desert of southwestern USA (BLINN et al, 1976). Winter rains entering flooded canyons at the lake's edge alter the ϵ min value from 0.224 to 0.733 as a mean annual range, and cause a shift in the most penetrating light from green towards red.

Transparency in the north basin of Lake Tanganyika is generally very great (DUBOIS, 1958; MELACK, 1976), with maximum 1% penetration depths of around 25 m compared with maxima of 13 m in Lake Turkana. When the Rivers Ruzizi and Malagarasi flood seasonally, during October, Lake Tanganyika becomes more turbid, and min shifts towards the red region.

Lake Malawi shows a 1% penetration depth of 40 m in October (BEAUCHAMP, 1953), which is reduced to ca 12 m in early October, apparently by greater densities of suspended solids and phytoplankton population.

Other African lakes with generally clear water include Lake Victoria. From the figures of LEVRING and FISH (1956), extinction coefficients of 0.29/m offshore and 0.49/m inshore, near Jinja, have been calculated. TALLING (1965) reports min to lie in the green waveband, between 0.165 offshore and 0.33 inshore, with higher values associated with denser algal populations

TALLING (*op. cit.*) reports that waters from Lakes Albert and Edward transmit green light most strongly with values of 0.35 for ε min in Lake Albert and 1.3 for Lake Edward. Seasonal increases in the turbidity of these lakes shifts the green attenuation closer to that of red light.

Highly productive waters in East Africa show much higher min values, with red light penetrating most, and blue light least. GANF and VINER (1973) report the trophogenic zone in shallow Lake George (mean depth ca 2.25 m) to be 0.75 m, and ε min values to range from 4-18. Most of the light attenuation, averaging 73% according to GANF (1972), is caused by high algal populations with densities of ca 205 g chlorophyll *a*/l, but regular cycles of strong wind-mixing introduce turbidity associated with temporarily suspended sediments.

MELACK and KILHAM (1974) report ε min values of 10 for Lake Nakuru, with red light penetrating most strongly. This lake similarly supports a dense algal standing stock. Very high concentrations of suspended silt in Lake Manyara, however, cause a similar effect, with accentuated attenuation in blue and green wavebands (see also JENKIN, 1936). TALLING *et al* (1973) report very high ε min values for the red waveband from Ethiopian soda lakes, ranging from 7.5 to 15.6 for Lake Kilotes and 13.6 to 25.5 for Lake Aranguadi.

Preliminary observations on the correlation between sonic-scattering layer depth and light intensity

Results

Several of the echo traces shown earlier (Plates 1.5-1.11) show a discrete layer generally situated from 4 to 20 m below the surface. The layer, referred to as the 'midwater scattering layer' was frequently divided into two or more sub-layers, spread over a depth zone of several metres. The depth of the middle sub-layer was used in the following calculations.

Investigations discussed in detail in a later section (Chapter 8, page 625) proved that the midwater scattering layer is biotic in origin and indicates the presence of small pelagic fish. It was also found that the depth at which the layer was situated varies with the underwater light climate, and for this reason the topic is introduced at this point in the report.

Cloudless skies are a common feature of the Lake Turkana climate and during the course of a particular cruise, light intensity at the water surface was generally steady. Data from two lakewide surveys were used in an attempt to correlate the depth of the 1% surface incident light and that of the scattering layer (Fig. 1.88). The correlation proves to be high significant, $P = < 0.25$, $r^2 = 0.94$, $F = 225.7$, and the relationship is expressed by the following equation:

$$y = 1.63 + 2.75x$$

Where y = depth of scattering layer in m and x = depth of 1% incident light in m.

Observations from Station H1 covering the period October 1972 to March 1975 have been analysed in a similar way (Fig. 1.89) but the results showed a less significant correlation ($P = < 0.25$, $r^2 = 0.555$, $F = 7.11$). The relationship is described by the equation $y = 6.11 + 1.58x$. However, the Station H1 data were more significantly related when $\log_{10}$ absolute light intensity at a depth of 3 m was plotted against the depth of the scattering layer (Fig. 1.90).

Discussion on scattering layer depths

It seems likely that the relatively poor results from the H1 observations (Fig. 1.89) are due to the wide variations in light and wave conditions encountered over the 30 month period. Evidence from the two lakewide surveys shown here indicates a close relationship between light intensity and the depth of the scattering layer (Fig. 1.88). The actual intensity of light at the scattering layer is not known due to the low sensitivity of the photocell at values below 0.1% of the surface incident light normally recorded on Lake Turkana.

The majority of reports on sonic-scattering layers are based on marine studies. McCARTNEY (1966) provides a useful recent review of earlier work. BODEN and KAMPA (1967) compared the ascent and descent of a particular level of light intensity in the sea with simultaneous observations on migrations of the pelagic fauna. Migrations were recorded with an echo-sounder and found to be controlled by the photoenvironment. Light is the primary variable affecting such migration, except where limits are imposed by physiological tolerances. DAVIS (1976) reported that adverse temperature gradients constituted barriers to light-initiated movement of the midwater scattering layer and BODEN and KAMPA (1965) found that reduced dissolved oxygen levels similarly limited movements.

During the present investigations, such potential barriers were not encountered on Lake Turkana, where the open waters are well oxygenated and close to isothermal throughout.

Water Chemistry

Introduction

Lake Turkana lies in an enclosed basin with no surface outflow. A relatively constant lake level is maintained by a balance between inflow and evaporation. As a result the concentration of solutes increases continually.

It was predictable that members of Teliki's expedition in 1888 would find that the water of the lake was disappointingly 'brackish' (VON HOHNEL, 1891). They found that with the addition of tartaric acid, the water effervesced strongly and concluded that it had a high soda content.

BEADLE (1932) carried out the first comprehensive analyses of water samples during the Cambridge Expedition of 1930/31. He confirmed that the waters were saline, but suggested that the concentration of salts was not as high as would be expected in a lake which had been enclosed for several thousand years. His results were augmented by workers from the E.A.F.F.R.O. laboratory at Jinja who made sporadic visits to the lake during the decades of 1950 and 1960 (FISH, 1953 and 1954; TALLING and TALLING, 1965) and by geologists from the Geological Survey of Kenya. DODSON (1968) reviews much of this later work.

On the basis of these previous results, which are summarised in Table 1.13 TALLING and TALLING (1965) placed Lake Turkana in Class II of their classification of East African lakes. Figure 1.91 illustrates the relationship between concentrations of major anions and conductivity for the various lakes and shows that the result for Lake Turkana lies within the general trend of the observations.

The relatively minor discrepancies between the analyses of previous workers on Lake Turkana (Table 1.13) are accounted for mainly by the changes which take place during the influx of freshwater from the River Omo. A major aim of the present investigation has been to study such seasonal and regional changes in greater detail, and to determine their effects on the productivity and biology of the flora and fauna. It was also hoped that the results would provide evidence concerning the rate of salinity increase within the closed basin of the lake.

Methods

Analyses of several major nutrient components were carried out at Lake Turkana but the majority of the chemical determinations were undertaken in the UK on stored samples.

(i) On site analyses

(a) Phosphate-phosphorus

The basic molybdenum-blue (stannous-chloride reduction) technique (A P H A 1965) was employed for orthophosphate determinations on filtered lake water, with added phosphate as an internal standard. Absorbance was measured spectrophotometrically using cells of 40 mm path length. The limit of detection was approximately 0.1 µg PO_4-P/1. Samples of glass distilled water, bore-hole water and tap water were also checked.

(b) Nitrate-nitrogen

Filtered lake water was analysed for nitrate-nitrogen using the method of WOOD et al (1967). Nitrate to nitrite reduction was carried out by passage over copperised cadmium filings in columns based on the original design of WOOD et al (op.cit.). The columns were made by the Physics Department of Nairobi University. The normal nitrite assay technique using sulphanilamide was followed with a limit of detection of 0.1 µg NO_3-N/1. Unreduced samples were also analysed to determine nitrite-nitrogen concentrations and when present nitrate-nitrogen was calculated from the difference.

Spectrophotometric determinations were carried out at the Ferguson's Gulf laboratory using a Pye Unicam SP 600 spectrophotometer with cells of 5, 10 and 40 mm path length. As the power pack supplied failed to stabilise the current from the generator sufficiently, the spectrophotometer lamp was driven directly from a 12 volt accumulator battery.

(c) Calcium and Magnesium

Calcium and magnesium analyses were carried out with a titrimetric method described by GOLTERMAN (1969) using Calcon, Eriochrome Black T and E D T A. The concentrations were so low that an automatic pipetting unit (Arnold R Howell Ltd.) had to be used for the titrations. The results were similar to those obtained by more accurate methods employed at a later date on stored samples in England.

(ii) Analyses carried out on stored samples

Over 200 samples of lake water taken from all parts of the lake were stored mainly in polythene bottles with either chloroform or sulphuric acid, and shipped to England for analysis. Additional unpreserved samples were also despatched.

Analyses of this material were carried out by Dr Ida Talling at the Freshwater Biological Associaton's Windermere laboratories. We are very grateful for her assistance.

The conductivity of the stored samples was checked against field measurements using a Leeds and Northrup conductivity meter (Model 4959), after adjustment to K 25°C. A small proportion of samples were found to have changed considerably and were consequently discarded. Certain samples had fallen significantly in conductivity but no obvious explanation can be given. Increases in conductivity due to evaporation were also noticed, but the majority of samples were found to have similar values to those measured in the field.

Chloride

Chloride concentrations were measured with an Amino-Cotlove automatic chloride titrator (American Instrument Co Ltd). Sample dilutions of 1:50 or 2:50 with deionised water were generally found to give the best results.

Thirty one samples were also measured by the potentiometric titration method with a silver electrode sensor, described by GOLTERMAN and CLYMO (1970) and adapted to read out on a Metrohm Titroprint automatic titrator. The two methods gave very similar results (within 10%).

Alkalinity

The potentiometric titration method described by MACKERETH *et al* (1977) was used with sample dilutions of 1:20.

Strong Acids

Total anions of strong acids (including Cl^-, SO_4^{2-}, NO_3^- and Fl^-) were measured using the ion-exchange method described by MACKERETH *et al* (in press). 20 ml of effluent were titrated with 0.01 N NaOH and the end point was determined by a Gran Plot. A 1:5 dilution of the sample was found to be adequate.

Potassium

A Unicam SP 900 flame-spectrophotometer was used at 777 nm. A dilution of 1:50 or 2:50 with deionised water was found to be satisfactory. 90 samples were also measured with an atomic-absorption spectrophotometer (Perkin Elmer 303) at 766.5 nm, which gave similar results (within 10%).

Sodium

A Unicam SP 900 flame-spectrophotometer was used at 592 nm. A dilution of 1:50 was found to be adequate. 90 samples were also analysed with an atomic-absorption spectrophotometer at 589 nm. The results were similar (within 10%).

Magnesium

Magnesium concentrations were determined by atomic-absorption spectrophotometry at 284.2 nm. 12.5 ml of an acidic solution of lanthanum 0.5N HCl ; 0.1% lanthanum were added to a 2.5 ml sample in a 50 ml volumetric flask and made up to 50 ml with deionised water.

Calcium

An atomic-absorption spectrophotometer was used at 422.7 nm. 12.5 ml of an acidic solution of lanthanum (see above) was added to a 25 ml sample in a 50 ml volumetric flask. This was made up to 50 ml with deionised water.

Iron (total Iron)

The method described by DAVISON and RIGG (1976) was used with a 50 ml sample. Interference from other solutes was determined using an internal iron standard, but levels were negligible with the volume used. A few samples were filtered with Whatman GF/C and GF/F glass fibre filters to measure the proportions particulate to dissolved iron.

Fluoride

Four samples were examined using an Orion 401 specific-ion meter (ionalyser), fluoride electrode model 94-09A (Orion) and a double junction reference electrode containing 0.25 M Na_2SO_4 in the outer sleeve. A dilution of 1:10 was found to be necessary. An initial reading was taken before a small volume of fluoride standard solution was added. The fluoride concentration was then re-measured so that the percentage recovery could be calculated and the results adjusted accordingly.

Results

The results of all chemical analyses carried out on samples collected during the present study are summarised in Table 1.14. Where several stations located in a particular sector of the lake were sampled during the same months, the data have been combined to give a mean value. The table (Table 1.14) thus shows variation in the chemical composition of the lake by sector and by season. Gaps exist mainly when the quantity of sample was too small for all the analyses to be carried out, or where the method of preservation was unsuitable (eg acid-preserved samples and 'strong acid' analysis).

A separate table (Table 1.15) shows a summary of the results of analyses carried out on samples taken from sites outside the main lake. Table 1.13 has been compiled from the results of previous studies.

The completed tables provide a comprehensive picture of the lake's water chemistry and the changes which take place during the influx of fresh water from the Omo River.

In order to check that the analyses were internally consistent and that they have accounted for all the major ions, the equivalents (in mq/L) were calculated and examples of individual samples are shown in Table 1.16. These examples show that the sums of cations and anions are similar but indicate a slight underestimate of the anionic component in certain cases. It is also evident that the analyses have accounted for all the major ions.

Major ions

In order of dominance by weight, $Na^+ \gg K^+ > Ca^{2+} > Mg^{2+}$ with sodium contributing over 95%. This situation is typical of many East African lakes where high salinities are found in closed basins (cf TALLING and TALLING, 1965) and in which the bi-valent ions (calcium and magnesium) occur. TALLING and TALLING (op. cit.) found that there are localised differences in the ionic ratios in East African lakes. The waters of lakes (such as Lake Turkana) in the Eastern arm of the Rift Valley have higher Na^+/K^+ ratios and higher Ca^{2+}/Mg^{2+} ratios than those in the Western Rift Valley. YURETICH (1976) has discussed these differences in relation to the geology of the catchment areas. He considers that the greater proportion of K^+ and Mg^{2+} in lakes of the Western Rift can probably be accounted for by the higher proportion of biotite and/or hornblend in the igneous rocks at their catchment areas. It has been pointed out earlier (page 12) that the volcanic rocks of the Omo River catchment area produce runoff waters which are rich in sodium.

Anions

The anionic composition is also similar to that found in other East African lakes which have high salinities, with bicarbonate and carbonate ions (expressed as total alkalinity) predominant. As the pH is ca 9.3, about 90% of the dissolved inorganic carbon is in the bicarbonate form (cf HUTCHINSON, 1957). Chloride is also an important anion but sulphate, fluoride, nitrate and phosphate ions are much less abundant. HUTCHINSON (1957) classified saline lakes on the basis of their ionic composition. By this criterion, Lake Turkana may be regarded as a chlorocarbonate lake.

Major changes in the ionic composition of the lake occurred only during the flood season and were confined to the

Northern Sector. This is demonstrated by comparisons of ionic concentrations of individual ions with the conductivity of the water shown in Figure 1.92 a-e. In most cases the increase in ionic concentration with conductivity is linear. Similar results were obtained by TALLING and TALLING (1965) who combined results from a large number of East African lakes. Notable exceptions to the linear increase are calcium and magnesium which appear to be lost to the sediments rapidly on entering the lake. It should be noted that although the increases are linear there is a change in the relative proportion of the various ions with increasing conductivity. The evidence proves that with the exception of chloride, ions tend to be lost by precipitation as the conductivity increases. With most ions the rate of loss is constant and it is possible to calculate the concentrations of the major components from the conductivity of the water. Exceptions to this rule are calcium, magnesium, iron, nitrate and phosphate. VISSER (1974), working on results of water analyses from numerous sites in both East and West Africa, found linear relationships between the concentration of major anions and the conductivity of the water, but only with levels up to 400 μS/cm.

Minor ions

The term 'minor' may be misleading when applied to ions which occur in low concentrations but which are of considerable biological importance.

Total iron concentrations derived from the analysis of unfiltered lake water varied from 2-3 mg/l in the Northern Sector to 0.4-0.6 mg/l in the open water of the Central Sector and 0.15-0.3 mg/l in the Southern Sector. The overall trend was, therefore, for iron concentrations to decrease southwards from the Omo River. Exceptionally high concentrations of ca 2 mg/l which were noted on the exposed west coast of the Central Sector may have been due to upward transport of particulate iron from the sediments resulting from turbulence. This mechanism had been suggested by TALLING and TALLING (1965) to explain why shallow lakes in East Africa have generally higher total iron concentration than the deeper lakes. The hypothesis is supported by further results from the present survey which indicate that filtered water had significantly lower iron concentrations than unfiltered water. The decrease in iron concentrations from north to south is probably caused by a loss of iron to the sediments. YURETICH (1976) has demonstrated a similar trend in the chemical composition of the sediments.

The concentration of dissolved silica and phosphate-phosphorous were also rather variable but the average concentration of 18.5 mg/l and 331 μg/l respectively are similar to the results presented by TALLING and TALLING (1965) for other East African lakes.

The least abundant of the nutrient ions was the nitrate and nitrite component. Frequently these ions were undetectable (i.e. less than μg/l). Maximum concentrations of 17.7 μg/l were noted in the Omo delta region. Both TALLING and

and TALLING (1965) and VISSER (1974) noted that nitrates are generally scarce in East African lakes. Rainwater, a notable source of nitrate, is unlikely to contribute more than a trace of this ion in the arid Lake Turkana region.

TALLING and RZOSKA (1967) describe how the Blue Nile derives considerable amounts of nitrate from the Ethiopian Highlands. It seems likely that the River Omo is also an important source of nitrogen in the Lake Turkana basin. No nitrate analyses were carried out on River Omo water during the present study but FISH (1953 - unpublished) obtained a value of 150 µg/l for nitrate nitrogen. VINER (1975) showed that nitrate concentrations in East African rivers varied considerably but his analyses of 13 rivers draining volcanic rocks in the Mt Elgon and Karamoja regions of eastern Uganda yield similar values with a mean of 269 µg/l for nitrate nitrogen.

Nitrate and nitrite nitrogen analyses carried out during the present study indicate that springs around the lake may provide significant localised sources. For example, Eliye Springs (30 µg/l) and Kalokol River (27 µg/l) contain much higher concentrations than the lake water. It is evident from the low levels of nitrate and nitrite nitrogen, both inshore and in the open water, that nitrates are very rapidly utilised. No nitrate was detected in the highly productive waters of Ferguson's Gulf despite a potentially abundant supply from the excreta of the rich avifauna, from cattle and goats and from the hetercystous blue-green algae.

Fluoride is also an important ion because of its reactive nature in biological systems. Its significance in East Africa has been discussed recently by KILHAM and HECKY (1973). Although only few analyses were made during the present study, the range of between 9-12 mg/l agrees with the results of DODSON (1963) shown in Table 1.13. Concentrations are somewhat higher than the level of 1 mg/l recommended by the American Public Health Association (1965). Levels above 10 mg/l are considered to be detrimental to human health, and future increases above the present level could have serious consequences. At present fluorosis is not a recognised problem in the Lake Turkana area. The full significance of fluoride as a factor limiting the distribution of organisms in the saline lakes of East Africa is not yet known. LA BARBERA and KILHAM (1975) note that copepods are not found in lakes in East Africa which have fluoride concentration greater than 1,064 mg/l.

A detailed discussion of the effects of the ions important as nutrients on the productivity of the lake, and their influence on the distribution of organisms will be given later.

Discussion

Evidence discussed in a previous section of this report shows that Lake Turkana has existed as an enclosed basin with no surface outflow for approximately 7500 years. BEADLE (1932 and 1972) has pointed out that in such a closed system higher salinities would be expected in the contemporary lake than is actually the case.

It is calculated from the dimensions shown in Table 1.1 and from an evaporation rate of 2.33 m/year that under the present climatic conditions, the inflow of water into the lake each year amounts to a volume of 18.6 km^3. A retention time of 13.4 years is calculated from this input. Under such circumstances, conductivity of the lake should rise by an amount equal to the conductivity of the inflowing river water every 13.4 years. The conductivity of the River Omo is approximately 80 µS/cm and the rate of increase in the lake should be about 6 µS/cm per year. On this basis present day lake conductivities of ca 3400 µS/cm would indicate that the basin had been enclosed for a maximum of 600 years, an estimate which is not supported by geological records.

Measurements of the conductivity of Lake Turkana span a period of 45 years but seasonal changes in salinity preclude comparisons which might have led to a more reliable estimate.

The most satisfatory estimate is provided by geological evidence BUTZER (1972) has shown that the lake basin has been enclosed for ca 7500 years. It is assumed that lake water at the time of closures was similar to that of the present inflow, then an increase of 3350 µS/cm has occurred during this period, equivalent to a rate of 0.45 µS/cm per year.

The marked difference between the rates of increase estimated from hydrological and geological evidence indicates that salt losses have been considerable. BOUCHARDEAU (1962) suggested that in the enclosed basin of Lake Chad, conductivities remained low due to the infiltration of water into a marginal system of sand dunes and sediments. Physical evidence to support the hypothesis was later found by DIELEMAN and RIDDER (1963). BEADLE (1974) suggested that a similar mechanism might exist in Lake Turkana on the sandy western shores of the lake. No relevant investigation was possible during the present project. It is thought, however, that since the lake lies in a relatively deep basin at the lowest point in the surrounding region of the Rift Valley, large scale water losses are unlikely.

Salt losses on a small scale occur during seasonal fluctuations in lake level. As the lake level drops, water is often isolated in lagoons which form behind sand bars, particularly on the exposed west shore. The lagoons evaporate and salt deposits tend to blow away inland in the strong southeasterly winds. Similar aerial losses of evaporates have been described for desert lakes by COLE (1968).

In Lake Turkana the most significant salt losses occur by sediment/water interactions. YURETICH (1976) has related the sediment mineralogy to water chemistry. He has shown that mineralisation processes can account for ionic losses in the following ways:

(i) Calcium is precipitated as calcite

(ii) Magnesium is probably utilised in the formation of montmorillonite from fluviate amorphous silicate material

(iii) Potassium is probably removed during the regrading of illite

(iv) Sodium is absorbed as an exchangeable cation in montmorillonite

Differential rates of loss for various ions are indicated by the data in Table 1.17. The ion least affected by precipitation or by other loss processes is chloride. It is interesting to compare the observed concentration factor of the chloride ion (Table 1.17) with a value estimated from geological evidence of the lake's recent history. Calculations have been based on the following assumptions:

(a) That 7500 y b p Lake Turkana had an area of 32,900 km (from Fig. 1.6), a volume of 1885 km and an evaporation rate of 1.4 m/year. It is assumed that conditions were 'fluvial' and the evaporation rate is based on data for the present day Lake Victoria (HURST, 1957). A retention time of 40.92 years has been calculated from these parameters.

(b) That the contemporary lake has a mean retention time of 13.4 years.

(c) That losses of chloride are negligible and may be ignored.

On the basis of the initial and final values quoted above, it is postulated that over the last 7500 years the mean retention time has been 27.2 years. Such a period would result in a concentration factor of 7500/27.2 or 276.2 due to the input of water from the catchment area. A further concentration factor of 7.5 should be added to take into account the reduction in volume of the lake from 1885 km ^{3} to 250 km ^{3} and the total concentration factor for chlorides is thus estimated to be 283.7. This compares favourably with the observed concentration factor of 309.6 (Table 1.17).

The results are even closer if a correction factor is applied to the observed values to compensate for the fact that the chloride content of Lake Turkana at the time of closure was almost certainly considerably higher than that of the inflowing river. If chloride concentrations in the lake were 30 mg/l (i.e. similar to current levels in Lake Albert) the observed concentration factor would fall to 291.5.

It is difficult to predict either the changes which will occur in Lake Turkana as the salinity increases or the rate at which these changes will occur. The results of TALLING and TALLING (1965) and KILHAM and HECKEY (1973) indicate that only minor alterations in the relative abundance of the ions are likely to take place. Potassium will probably increase in abundance relative to sodium, but calcium and magnesium levels will remain low. Changes in anionic composition are likely to be small. HUTCHINSON (1957) and COLE (1968) both demonstrate the tendency in chlorocarbonate lakes for the relative abundance of chloride to increase with increasing salinity.

Crater Lake A on Central Island provides an opportunity to study changes in ionic composition as the lake water becomes concentrated. The crater lake with a conductivity of 10,000 μg/cm is replenished by underground seepage from the main lake. Chemical analyses by BEADLE (1932) are shown in Table 1.13 and results from the present investigations in Table 1.15. Changes in the cationic composition have been slight as demonstrated by Table 1.18.

The affects of such changes in chemical composition on the rate of loss of ions to the sediments is not known but it seems likely that the conductivity of the main lake will continue to increase by about 0.45 μS/cm per year. It is considered that this rate of increase is sufficiently slow for it to be ignored as a factor likely to affect the fishery in the foreseeable future. However, any changes which might take place within the basin resulting in changes in the composition of the major inputs, particularly the River Omo, should be monitored.

SUMMARY

The geographical features and geological history of Lake Turkana are described with details of the possible changes which have taken place since its connection to the Nile system via the Lotogippi swamps was severed ca 3,500 y b p.

Meteorological data for 1972-75, recorded at a station on the lake shore, are discussed. The mean daily air temperature was 29.3 C and the annual rainfall was less than 250 mm. Strong prevailing south-easterly winds were a prominent climatic feature. Mean wind speed was much higher in the south of the lake where a value of 760 Km/24 hrs was recorded, compared with 299 Km/24 hrs in the Central Sector. Marked diel changes in the wind regime were noted and whereas strong winds blew on 82% of mornings, calm conditions were recorded on 82% of the afternoons. Relative humidity averaged 60% and evaporation 2.3 m/year.

Investigations of the physical and chemical limnology proved that the lake is well-mixed by the strong south-easterly winds. Vertical temperature and oxygen stratification was minimal with oxygen concentrations ranging from 5.0 to 6.5 mg/l at a depth of 80 m compared with 6.8 to 8.4 mg/l at the surface. Water conductivity varied considerably on a seasonal basis due to influence of fresh water from the River Omo between June and October each year. The mean conductivity of the lake was ca 3500 µS/cm K25 C, ranging from 200 µS/cm near the Omo delta during the flood season to over 4700 µS/cm in Ferguson's Gulf. Conductivity changes were used to follow the pattern of water circulation in the lake. Further evidence was provided by E R T S satellite photographs and by subsurface light penetration measurements.

Results of chemical analyses show that the lake is a sodium carbonate lake. The ionic composition suggests that appreciable quantities of most ions are lost to the sediments and that sediment water interactions are responsible for maintaining a relatively low conductivity. Observations on the concentrations of nutrient ions indicate that nitrates are limiting the lake's productivity.

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TABLE 1.1

A summary of data relating to the size, area and volume of Lake Turkana. Estimates of the surface area of the lake included between successive depth contours, and of the volume of water contained in different depth layers, are given below. The observations are based on the 10th September 1972 lake level.

(i) Length = 257 km

(ii) Breadth mean = 31.12 km
max. = 44 km
min. = 13 km

(iii) Depth mean = 31.4 m
max. = 114 m

(iv) Area = 7560 km^2

(v) Volume = 237.36 km^3

(vi) Height a.m.s.l. = 365.4 ± 5 m

Depth (m)	Area (km^2)	% area	Volume (km^3)	% volume
0-10	1619	21.4	67.51	28.4
10-20	1199	15.9	53.41	22.5
20-30	1269	16.8	41.07	17.3
30-40	1005	13.3	29.69	12.5
40-50	698	9.2	21.18	8.9
50-60	809	10.7	13.64	5.8
60-70	530	7.0	6.95	2.9
70-80	270	3.6	2.95	1.2
80-90	147	2.0	0.87	0.4
90-100	11	0.1	0.08	+
100-110	2	+	0.01	+
110 +	+	+	+	+
Total	7560		237.36	

TABLE 1.2

Estimates of the area of Ferguson's Gulf at various times during the period 1930-1975

Date	Area (km^2)	Volume ($m^3 x 10^6$)	Reference	Source
Dec-Jan 1930-31	40.42	69.39	Worthington (1932)	Plane table map
20 Aug 1958	25.62		Survey of Kenya	RAF map V13A 684
17 Jan 1972	39.56		RAF V13B 805	Aerial photograph
10 Sept 1972	38.10		ERTS/81049072135A000	Satellite photograph
27 Dec 1972	37.41		ERTS/81157072235A000	Satellite photograph
1 Feb 1973	36.49		ERTS/81193072215N000	Satellite photograph
8 Mar 1975	32.41		ERTS/82045071035N000	Satellite photograph
14 Apr 1975	31.50	24.36	ERTS	Satellite photograph
6 June 1975	29.61		ERTS/821350710250000	Satellite photograph
12 July 1975	30.10		ERTS/821710710150000	Satellite photograph
3 Dec 1975	35.13		ERTS/823150708250000	Satellite photograph

TABLE 1.3

Estimates of the area (in km^2) of the Lake Turkana basin and its constituent catchment regions made during the present observations compared with earlier calculations of BUTZER (1971) and YURETICH (1976). An assessment of the percentage land surface occupied by the main rock types in each catchment from YURETICH (op. cit.) is also provided.

	Areas in km^2			Rock type - % Surface area		
Region	BUTZER(1971)	YURETICH(1976)	Present study	Volcanic	Basement	Alluvial
Omo basin	73,000	87,000	74,000	68	7	25
Sanderson's Gulf	11,000					
Ephemeral rivers	15,000	13,500	9,900	77	3	20
Turkwell basin	24,500	42,000	39,400	28	43	32
Lomenyangaparat basin	3,500					
Kerio basin	13,500					
Lake surface	7,500	7,500	7,560			
TOTAL	148,000	150,000	130,860			

TABLE 1.4

A summary of the physical and mineralogical characteristics of the openwater sediments based on analyses made by YURETICH, 1976, on representative samples covering all sectors of the lake.

Size fraction	% by weight mean	range	Minerals	% by weight within size fraction
Clay	71.4	15.5-97.0	Montmorillonite	40
			Illite	9
			Kaolinite	16
			Quartz	28
			Feldspar	8
Silt	25.8	3.2-80.0	Calcite	39
			Quartz	26
			Feldspar	24
			Heavy minerals	11
Sand	2.8	0.01-27.6	(a) Metamorphic:	
			Quartz	
			Feldspar	
			Blue/green Amphiboles	
			(b) Volcanic:	
			Red/brown Hornblend	
			and volcanic rock fragments	

TABLE 1.5

Estimates of the rate of the accumulation of seston in gm/m^2/day (dry weight) based on data from sediment traps deployed in the Longech and Central Island areas of the Central Sector.

		Accumulation of seston gm/m^2/day (dry weight)	
Site	Date	Top tube	Bottom tube
Central Island	July 74	22.7	31.5
Central Island	Jul-Aug 74	16.6	19.3
Central Island	Sep-Nov 74	9.5	(lost)
Longech outer buoy	Dec 74	13.5	17.1
Longech outer buoy	Jan 75	8.3	11.3

Summary

Locality	Mean sedimentation rate gm/m^2/day (dry weight)
Central Island	19.9
Longech	12.5
Both sites	12.7

If the density of the sedimented material is taken to be 2.2 and the pore water content 50% (YURETICH, 1976), the overall mean of 12.7 gm/m^2/day is equivalent to a rate of sedimentation of 4.232mm/year.

TABLE 1.6

TABLE 1.6

Details of permanent islands noted during the present study. The reference numbers refer to annotations on Fig 1.3.

Region	Ref. N^{o}	Name	Position	Area (km^{2})	Elevation (m)	Type
North	1	North Island	HBH 391484	2.3	122 (1)	Volcanic with varied shoreline including lava flows, cliffs of compacted ash and sandy beaches
Allia Bay	2	Skimmer Bank	HBH 592083	0.1	5	Low gravelly with rocky outcrops
	3	Low Island	HBH 602075	0.1	5	Low gravelly with rocky outcrops
Central	4	Central Island	HBB 855385	4.8	183 (2)	Volcanic with varied shoreline including cliffs of compacted ash, basalt boulders, sand and gravel
	5	Satellites	HBB 378846	0.1	5	Flat, basaltic rocks and boulders
			HBB 396834	0.1	15	Steep, compacted ash
			HBB 400830	0.1	15	Steep, compacted ash
			HBB 402825	0.1	15	Steep, compacted ash
Turkwell-Kerio Basin	6	Otus Island	HBB 663516	0.1	5	Flat, basaltic rocks and stones with a little gravel
Southern	7	Elavto Island	HBC 010185	0.1	5	Low, rocky, much broken
	8	Mekeme Island	HBC 080185	0.1	10	Domed, basaltic
	9	El Molo (i)	HBC 103134	0.3	25	Basaltic with stony beaches interspersed with low cliffs
	10	Islands (ii)	HBC 105151	0.65	30	Basaltic with stony beaches interspersed with low cliffs
	11	South Island	HAP 995915	36.95	275 (3)	Volcanic, varied coastline including jagged lava flows, cones of compacted ash, often broken to give precipitous cliffs and beaches of sand and gravel

contd./

TABLE 1.6 (contd.)

12	Offshore Islets				
	Nanet	HAP 990990	0.1	40	Steep, compacted ash
	Ekinyang	HAP 987985	0.1	10	Steep, compacted ash
	Nan	HAP 980974	0.1	30	Steep, compacted ash
	Fang	HAR 000977	0.1	15	Steep, compacted ash
	Enwaite	HAR 025916	0.7	9	Flat, compacted ash
	White Rock	HAP 976859	0.1	5	Steep, compacted ash

References (1) BROWN and CARMICHAEL, 1971
(2) WORTHINGTON, 1932
(3) FUCHS, 1939

TABLE 1.7

Records of monthly rainfall in mm recorded at the fisheries station, Kalakol, and at the meteorological station, Longech, during 1973 and 1974. Data for the two stations have been combined for the two years and mean values for Lodwar for the years 1947-54 are included for comparison.

	1973		1974		Both stations	Lodwar
	Longech	Kalakol	Longech	Kalakol	1973-74	1947-54
January	0.5	-	3.1	0.5	1.0	1.0
February	-	-	4.1	14.7	4.8	2.5
March	-	-	47.3	56.6	25.9	20.3
April	47.0	34.9	45.6	23.4	37.8	60.9
May	36.7	34.0	2.1	-	18.2	22.9
June	-	-	-	-	-	2.5
July	67.0	11.3	16.0	21.5	28.9	12.7
August	-	-	96.5	84.3	45.2	1.3
September	41.3	10.0	-	-	12.8	1.0
October	10.2	2.2	-	-	3.1	7.6
November	24.4	37.0	-	-	15.4	7.6
December	-	-	-	-	-	10.3
TOTAL	227.1	129.4	214.7	201.0	193.1	150.6

TABLE 1.8

TABLE 1.8

Correlation matrix for various meteorological factors recorded during a period of 75 days during 1974 at the Longech meteorological station.

Meteorological factors	Wind speed (km/24hrs)	Pan evaporation (mm)	% relative humidity	Maximum temperature (^{o}C)
Wind speed	1.0000			
Pan evaporation	0.4839	1.0000		
Relative humidity	- 0.0822	- 0.1770	1.0000	
Maximum temperature	- 0.1650	- 0.1575	- 0.2269	1.0000

TABLE 1.9

Mean monthly maximum air temperature in °C, recorded at three sites near the lake to illustrate the seasonal variations shown by long term records.

Month	Lodwar (8 yrs)	Lokitaung (8 yrs)	Longech (3 yrs)	Season
Jan	36.1	33.3	33.0	1 (Hot)
Feb	36.7	33.8	33.4	
March	36.7	33.3	33.2	
April	35.0	31.1	32.1	2 (Major rains)
May	35.0	31.1	31.9	
June	34.4	31.1	32.3	
July	33.3	30.5	31.5	3 (Cool)
Aug	33.3	30.5	31.8	
Sep	35.0	31.6	32.3	4 (Minor rains)
Oct	35.6	31.6	32.9	
Nov	35.0	32.2	32.3	
Dec	35.0	31.6	33.3	

TABLE 1.11

To show the importance of relatively small temperature differences in relation to density in a tropical lake compared with a stratified temperate lake. The densities have been adjusted to compensate for a salinity of 2.48^{o}/oo in Lake Turkana. References: (a) MORTIMER, 1941 ; (b) present study.

Lake	Temperature (^{o}C)	Depth (m)	Temperature difference (^{o}C)	Density (g/ml)	Density difference (g/ml x 10^{5})	Ref.
Esthwaithe	20.0	0	8.5	0.99821	134	(a)
August 1939	11.5	15		0.99955		
Turkana	29.4	0	4.0	0.99792	105	(b)
May 1973	25.4	80		0.99897		

TABLE 1.13

Summarising the results of previous water analyses carried out on Lake Turkana and the inflowing rivers.

N = Northern Sector, C = Central Sector, T = Turkwell Sector, S = Southern Sector, FG = Ferguson's Gulf, CL'A' = Crater Lake A, Central Island).

Year	Source	No. of samples	Sector /site	Conductivity µS/cm (25°C)	pH	Na^+ (mg/l)	K^+ (mg/l)	Ca^{2+} (mg/l)	Mg^{2+} (mg/l)	Alkalinity (meq/l)	Cl^- (mg/l)	SO_4^{2-} (mg/l)	F^- (mg/l)	SiO_2 (mg/l)	Ammonia (a) saline (mg/l)	Ammonia (b) albumenoid (mg/l)	NO_3-N (µg/l)	PO_4-P (mg/l)	Total iron (µg/l)
Lake :																			
1931	BEADLE (1932)	-	C	2860	9.5	770	23.0	5.0	4.0	21.7	429	56	-	4.2	-	-	-	1.64	-
1953	EAFRO (unpubl.)	-	C	-	9.62	-	-	5.53	5.3	21.5	307	59.2	-	25.6	-	-	0	1.64	420
1954	FISH (1954)	1	N	3190	9.5	-	-	2.45	2.4	23.0	245	2.0	-	72.0	-	-	0.15	2.0	trace
1956-7	DODSON (1963)	8	N,C,S	-	-	-	-	7.6	6.1	-	437	34	9.6	66.5	0.40	0.40	trace	-	-
1956-7	DODSON (1963)	1	FG	-	-	-	-	-	-	-	520	50	8.6	3.0	0.50	0.36	trace	-	700
1961	TALLING (1956)	-	C	3630	-	810	21.0	5.7	3.0	24.5	475	64	-	18.0	-	-	-	2.6	-
1973-4	YURETICH (1976)	23	N,C,T,S	-	9.2	753	17.6	4.7	2.3	19.0	514	39	-	18.5	-	-	-	-	30
Rivers :																			
1954	FISH (1954)	1	Omo	80	-	-	-	8.0	1.05	8.4	trace	-	-	26.0	-	-	0.3	0.05	5
1956-7	DODSON (1963)	1	Omo	-	-	-	-	1.1	0.66	2.5	2.8	trace	-	-	-	-	-	-	-
1975	YURETICH (1976)	3	Omo	-	7.0	9.7	1.8	9.5	3.6	-	2.7	-	-	-	-	-	-	-	18
1975	YURETICH (1976)	1	Kerio	-	7.2	35.6	4.9	23.3	4.2	-	18.5	-	-	-	-	-	-	-	-
Others :																			
1931	BEADLE (1932)	1	CL'A'	8100	9.5	2114	118.0	13	36	1700 (mg/l con.)	1300	46	-	-	-	-	-	0.36	-

TABLE 1.14

Showing the results of analyses carried out on the waters of the open lake during the present survey. Observations are arranged in chronological order. During each sampling period, data from all sites within a particular lake sector have been combined and the mean concentration is given in the table together with the number of samples in italics, and the range in brackets below. Abbreviations for the various sectors are the same as in Table 1.13.

Date	No. of samples	No. of sites	Sector or Station	Conductivity µS/cm (25°C)	Na^+ (mg/l)	K^+ (mg/l)	Ca^{2+} (mg/l)	Mg^{2+} (mg/l)	Alkalinity (meq/l)	Cl^- (mg/l)	F^- (mg/l)	NO_3-N (µg/l)	PO_4-P (µg/l)	Total iron (g/l)
Mar 73	1	1	S	-	887	21.5	-	-	-	430	-	-	-	-
Jul 73	8	4	T	-	857 (6) (798-887)	22.5 (8) (20.5-24.4)	2.8 (4) (2.8-3.2)	3.3 (5) (2.3-3.9)	-	433 (6) (423-440)	-	-	573 (6) (254-780)	838 (5) (1100-580)
Jul 73	5	2	S	-	922 (5) (886-822)	23.3 (5) (22.5-24.4)	1.3 (1)	2.4 (1)	-	455 (5) (438-489)	-	-	453 (7) (178-786)	778 (5) (490-1030)
17 Aug 73	1	1	H1	-	769	21.9	4.6	3.0	-	-	-	-	-	-
30 Aug 73	24	0	C	-	-	-	-	-	-	-	-	6.8 (8) (0-15.5)	277 (24) (178-358)	-
18 Sep 73	8	1	H1	3451	777 (7) (736-814)	23.7 (8) (21.5-28.5)	5.5 (7) (4.9-6.0)	3.4 (7) (3 3-3.6)	-	-	-	-	-	891 (1)
20 Sep 73	7	1	H1	-	-	-	-	-	-	-	-	-	138 (7) (109-181)	-
Oct 73	2	2	Omo	-	-	-	-	-	-	-	-	17.7 (2)	-	-
Oct 73	2	2	N	3100	-	-	-	-	-	-	-	9.3 (2)	-	-
Oct 73	1	1	C	3392	783 (1)	19.2 (1)	5.1 (1)	3.5 (1)	-	-	-	-	-	1977 (4) (1680-4300)
Oct 73	4	1	T	3565	-	22.8 (2)	4.8 (2)	3.4 (2)	-	-	-	-	-	-
Oct 73	8	2	S	3597	922 (2)	29.1 (2)	4.5 (2)	3.4 (2)	-	-	-	-	-	1798 (6) (570-3340)
24 Feb 74	8	1	H1	3603	829 (8)	27.7 (6)	6.5 (1)	3.8 (1)	-	-	-	-	-	-
17 Apr 74	14	5	C	-	761 (5) (738-805)	20.1 (5) (19.4-22.7)	5.8 (1)	2.8 (1)	-	389 (14) (360-414)	-			617 (2) (515-720)
20 Jul 74	1	1	Omo	2187	448	10.8	5.2	2.3	15.5	279	-	-	-	-
Jul 74	3	3	N	2481	873 (1)	23.5 (1)	3.6 (1)	-	25.2 (2)	463 (3)	-	-	-	440
Jul 74	4	4	C	3578	920 (2)	23.65 (2)	4.2 (1)	3.5 (1)	21.4 (3)	481 (3)	11.0 (1)	5.43 (7)	-	771 (1)
Jul 74	4	4	T	3802	919 (2)	24.6 (2)	3.9 (1)	3 2 (1)	25.7 (3)	475 (4)	-	-	-	-
Jul 74	3	3	S	3717	-	-	3.8 (2)	2.0 (2)	20.1 (3)	485 (3)	-	-	-	-
Aug 74	1	1	Omo	-	438	10.9	6.4	2.6	-	206	-	-	-	10645
Aug 74	1	1	Omo	2810	711	19.2	5.2	2.0	-	403	-	1.36	-	-
Aug 74	2	2	N	3500	773 (1)	28.1 (1)	5.9 (2)	3.15 (2)	-	-	-	0 (2)	-	1865
Aug 74	2	1	C	3525	898 (2)	23.3 (2)	4.5 (1)	2.2 (1)	-	497 (2)	-	-	-	-
Aug 74	1	1	S	3610	918	24.0	4.4	2.3	26.8	520	-	-	-	-
Feb 75	21	8	C	3475	770 (20) (725-797)	20.6 (20) (19.8-22.5)	5.41 (9) (5.2-5.5)	3.27 (18) (2.9-3.5)	21.0 (20) (19.5-22.9)	408 (20)	-	-	-	695 (17) (271-1395)
Mar 75	1	1	Omo	1056	252	9.0	1.9	1.7	6.2	174	-	-	-	1504
Mar 75	1	1	N	3440	814	21.5	2.3	2.2	20.1	445	10.0	-	-	1090
Mar 75	7	7	C	3451	799 (7) (756-860)	21.6 (7) (19.6-29.3)	4.2 (6) (3.5-5.1)	2.9 (7) (2.2-3.2)	20.9 (7) (20.5-21.3)	450 (7) (432-466)	-	-	-	1279 (6) (188-2810)
Mar 75	2	2	T	3510	851 (2)	21.3 (2)	3.8 (1)	3.41 (1)	-	447.5 (2)	-	-	-	380 (2)
Mar 75	16	5	S	3559	896 (16) (886-918)	23.9 (18) (22.5-28.9)	3.40 (15) (2.7-4.4)	3.30 (15) (2.2-3.7)	22.4 (16) (21.3-24.4)	484 (16) (424-512)	10.0 (1)	-	-	262 (14) (193-323)
Jun 75	2	2	T	3526	814 (2)	21.0	5.35)	3.10	22.89	410	-	-	-	300

TABLE 1.15

Analyses of water collected during the present investigations from Ferguson's Gulf and from other locations in the region of Lake Turkana, but outside the main lake.

(Y) = from YURETICH (1976)

Date	No. of samples	No. of sites	Site	Conductivity µS/cm (25°)	Na^+ (mg/1	K^+ (mg/1)	Ca^{2+} (mg/1)	Mg^{2+} (mg/1)	Alkalinity (meq/1)	Cl^- (mg/1)	F^- (mg/1)	NO_3-N (µg/1)	PO_4-P (µg/1)	Total iron (µg/1)
Jul 74	1	1	East Ferguson's Gulf	-	1042	26.0	5.3	2.4	-	524	-	0	-	489
	1	1	South east Ferguson's Gulf	-	-	-	-	-	-	-	-	0	273	-
2 Jul 74	1	1	Central Ferguson's Gulf	-	915	21.5	5.5	2.2	-	-	-	0	-	553
Mar 75	1	1	Loiengalani Springs	554	89.7	47	-	-	4.27	39	-	-	-	-
Aug 73	1	1	Eliye Springs	-	183(Y)	1.5(Y)	2.5(Y)	0.3(Y)	-	10.3(Y)	-	30	-	-
Aug 73	1	1	Audach Springs	-	99(Y)	1.1(Y)	2.3(Y)	1.4(Y)	-	8.4(Y)	-	11.5	-	-
Mar 75	2	2	Kalakol Gorge pools (a)	850	193	7.8	7.8	3.6	4.89	76	-	-	-	-
			(b)	803	175.5	5.9	11.6	5.1	4.37	66	0.80	-	-	1185
Jul 75	1	1	Crater Lake A, Central Island	9540	-	-	-	-	63.4	1527	-	-	-	-
			Kalakol tap water	-	-	-	-	-	-	-	-	27.0	-	-

TABLE 1.16

TABLE 1.16

Showing the ionic balance of selected water samples collected from the main lake during the present investigations.

			Conductivity										
Date	Sector	Depth (m)	Field µS/cm	Laboratory (25°C)	Strong acids* (meq/l)	Alkalinity (meq/l	Chloride (meq/l	Calcium (meq/l)	Magnesium (meq/l)	Sodium (meq/l)	Potassium (meq/l)	Total Anions (meq/l)	Total Cations (meq/l)
8/73	C	0	-	3748	15.56	25.40	14.20	0.21	0.17	39.15	0.60	40.96	40.13
8/73	C	0	-	3581	15.99	24.19	13.80	0.21	0.28	41.40	0.63	40.18	42.42
8/73	T	0	-	3377	13.83	23.50	12.50	0.21	0.28	39.00	0.50	37.33	39.59
24/2/75	Omo	0	1056	1159	4.68	6.22	4.45	0.10	0.14	10.50	0.23	10.90	10.97
24/2/75	C	5	3450	3375	12.45	20.90	11.45	0.24	0.27	32.85	0.50	33.35	33.86
12/3/75	S	25	3550	3632	14.34	23.08	13.40	0.22	0.28	39.90	0.74	37.42	41.40
12/3/75	S	50	3600	3618	14.34	23.10	13.60	0.17	0.31	39.10	0.58	37.44	40.15
13/3/75	S	100	3600	3628	14.83	21.28	14.20	0.14	0.31	38.50	0.58	36.21	39.50

* Strong acids include Cl^-, SO_4^{2-}, NO_3^- and F^-

TABLE 1.17

Showing changes in the concentration of major ions between the River Omo and Lake Turkana.

Based on the figures in YURETICH (1976) with an 80% loading to flood season conditions.

Ion	Average R. Omo concentration	Average L. Turkana concentration	Concentration factor
	mg/l	mg/l	
Cl^-	1.66	514	309.64
Na^+	6.83	753	110.24
K^+	1.38	17.6	12.75
Mg^{2+}	2.74	2.3	0.839
Ca^{2+}	8.79	4.7	0.534

TABLE 1.18

Comparison of the chemistry of Lake Turkana and Crater Lake A, Central Island, showing the proportion by weight of each cation expressed as a percentage of the total cations.

	Na^+	K^+	Ca^+	Mg^{2+}	Conductivity µs/cm
Main lake	96.5	2.5	0.51	0.35	3450
Crater Lake A	92.7	3.1	0.56	1.50	10000

CHAPTER 2

STUDIES ON ALGAL DYNAMICS AND PRIMARY PRODUCTIVITY IN LAKE TURKANA

by
B.J. Harbott

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A SYNOPSIS OF PRIMARY PRODUCTION RESULTS FROM LAKE TURKANA

SUMMARY

REFERENCES

2. STUDIES ON ALGAL DYNAMICS AND PRIMARY PRODUCTIVITY IN LAKE TURKANA

B J Harbott

INTRODUCTION

Compared to other major African lakes, the algae of Lake Turkana have received little attention from earlier workers and no estimates of primary productivity have been published. The remoteness and inhospitable nature of the basin have probably contributed to this situation. Most of the pioneer algology on Lake Turkana was carried out by the 1930-31 Cambridge University Expedition to the East African Lakes, in the vicinity of Ferguson's Gulf and Central Island (BEADLE, 1932; RICH, 1933). Net and grab samples were collected from both inshore and offshore sites and the results, analysed by RICH (op. cit.), provide an invaluable background to the present work. Lists of species were provided for all sites investigated and the filamentous blue-green alga Hormidium subtile was found to be the dominant species in the openwater plankton.

La Mission Scientifique de l'Omo (BACHMANN, 1938) collected algal material from the shallow northern inshore regions but reported few species not encountered by RICH (1933). The centric diatom Coscinodiscus rudolfii was stated to be typical of the phytoplankton of the lake, but most of the algae identified in the material of the Omo Expedition were littoral, and the genus Rhopalodia frequently dominated the associations (see also ROSS, 1953). Previously published algal records are given in Table 2.1.

SCOPE OF THE PRESENT INVESTIGATIONS

Algal studies were undertaken to identify the major species and to investigate fluctuations in population, both temporally and spatially. Estimates of biomass and productivity were made in order to provide information on basic organic production and on available algal food sources for higher trophic levels.

MATERIALS AND METHODS

The insulated water-bottles used for temperature determinations and water-sample collections (see pages 35 to 36) also served for sampling algae at discrete depths. Where algal material, but no information on temperature, was required, a modified plastic Kemmerer bottle of 6 litres capacity (G M Mfg, Chicago, USA), suspended from the 4 mm wire of the hydrographic winch, was used. Integrated plankton sampling was attempted with a 10 m rubber hose of 3 cm internal diameter, but this method failed to give satisfactory results and was soon discontinued. Algal samples were also obtained with a Clarke-Bumpus remotely-operated plankton sampler with a No 3 mesh (ca 60 µm pore size) net. This was used for sampling both horizontally and vertically, and collections provided material for algal and invertebrate analyses. All samples were preserved with a Lugols' iodine and formaldehyde solution.

Primary productivity in the openwater was estimated by means of the light and dark bottle technique. Water was collected from discrete depths, enclosed in 150 ml or 250 ml glass flasks and resuspended in an array of 2 light and 2 dark bottles at the collection depths. Exposure periods were generally in excess of one hour, during which time the frames were marked by a buoyed flag visible up to ca 8 km from R V HALCYON. Dissolved oxygen concentrations were determined using a modified Winkler technique (see page 35) in the laboratory aboard ship. Effervescence during acidification did not cause great problems, and little if any iodate was lost. Titrations were performed against 0.005 N potassium thiosulphate, using starch as an indicator.

Supplementary information was obtained by incubating samples in shaded water-baths on the deck of R V HALCYON when time or weather conditions did not allow the determination of in situ rates. This method was used only at very few sites.

Samples for chlorophyll a analysis were filtered onto magnesium carbonate beds, supported by Whatman G F C papers and stored frozen when necessary. Pigment extractions and measurements were performed following the method of GOLTERMAN (1969), using a Pye-Unicam SP600 series 2 spectrophotometer.

The light and dark enclosure method was also used to study primary productivity by the littoral flora. Epibenthic algae were covered by clear and foil-darkened flasks or funnels to determine areal productivity, while samples of water collected over the sites were incubated in paired flasks resting on the substrate or fixed, midwater, to a retort stand.

Macrophytic/epiphytic community production was estimated for single plants of Potamogeton pectinatus in thin-walled perspex tubes of 6 cm internal diameter, pressed into the substrate until their tops were level with the water surface, when they were stoppered. After incubation for periods between 60 and 90 minutes, the bases of the tubes and plants were cut, the plants carefully withdrawn and the bottoms sealed, all underwater. A modified Winkler oxygen determination method was run against the E I L dissolved oxygen meter to estimate changes in oxygen content of the water.

Dry weights of macrophytes and suspended algae were determined by drying primarily in air, then in a vacuum oven to constant weight at 70°C.

Background observations and records of data relating to physical and chemical parameters were recorded concurrently during field work. Methods and results are described elsewhere in this report (see Chapter 1 pages 35 to 66).

Carbon, hydrogen and nitrogen analyses of preserved algae were performed at the Ferry House, Windermere, England, using a Hewlett-Packard 185 analyser. Comparisons against a modified wet-dichromate method of carbon analysis (A P H A, Washington, USA, 1975) were also made.

Algal material was identified and counted using two main techniques. Samples collected with water bottles or integrated tubes were sedimented in tubes of from 2 ml to 50 ml capacity, and scrutinised under an inverted microscope. Where necessary, larger volumes of up to 200 ml were concentrated for counting in cylinders and flasks before being transferred to the smaller sedimentation tubes. High algal densities necessitated dilution or 2-stage counting. The latter method involved preliminary numbers being determined for dense, larger phytoplankters, e.g. Microcystis aeruginosa, M.flos-aquae and Botryococcus braunii, in Sedgewick-Rafter cells followed by counts of micro- and nanno- plankton using the inverted microscope.

Material collected with the Clarke-Bumpus sampler was diluted to a known volume, usually 200 or 400 ml, mixed in a polygonal-walled chamber with a magnetic stirrer, and subsampled with syringes. Four 5 ml subsamples were taken using the split-half technique and bulked into two 10 ml clip-top jars. These subsamples were then counted in the Sedgewick-Rafter cells.

Algae were identified to species level whenever possible using a Leitz SM-lux compound microscope with phase contrast illumination. The reference texts of BOURELLY (1966, 1968 and 1970, DAMAS (1937), DESIKACHARY (1959), HUSTEDT (1949) and SMITH (1950) were consulted for idenification as was the Fritsch Collection at Ferry House.

During counting and identification, considerable variation in size and shape was observed in most forms. Green and blue-green algae exhibited the greatest variety in colony dimensions and form, although diatoms also ranged greatly in size. Algal occurrence based solely on numbers would have led to gross inaccuracies, especially for the more massive forms. For this reason, estimates were made of mean colony or cell volume by trigonometry or by counting single cells in disrupted colonies. Disruption was effected by ultra-sonication of samples using an 'Acoustica' water bath and by dissolution of mucilage envelopes with organic solvents. These methods were not consistenly successful, but no satisfactory reason for the failure of disruption became evident. There was, however, a tendency for material which retained a deep purple colour from the Lugol's iodine to fractionate most readily. Sufficient information was available from parallel disintegration and direct measurement techniques to enable the latter to be used as a general method of cell volume determination.

DISCUSSION OF METHODS

As shown in Chapter 1, the climate of the Lake Turkana region varied little from season to season and the temperature regime of the lake was correspondingly stable. However, marked seasonal changes occurred within the lake as a result of the regular annual flood cycle of the River Omo, bringing suspended and dissolved material in fresher water into contact with the lake water. A further source of suspended material was created by the persistent, strong south-easterly winds which carried fine particles from the surrounding shore into the lake. Combinations of strong winds maintaining high quantities of solids in suspension, and generally low algal densities over much of the lake, added to the problems involved in the implementation and interpretation of algal studies.

Sedimentation of suspended material in counting chambers frequently hindered counting and identification. Non-algal particles covered at least as wide a size range as the algae, and it was therefore impossible to use filtration techniques for separation. Such particles often clogged the filters employed for chlorophyll a determinations. It was mainly for this reason that the integrated 10 m hose technique referred to above proved ineffective.

Net hauls were not quantitative for all the algal species present, but since large quantities of water were sampled, even in short vertical hauls, more reliable results were obtained for the larger, generally scarcer, species. In an attempt to overcome inconsistencies, net hauls and unconcentrated bottle samples were taken from the same depth at each sampling station and the results were corrected against each other to provide a basis for final counts. No fixed relationships between counts of algae from unconcentrated samples and net samples were used, as the factors varied from site to site and month to month, with changes in algal densities and cell or colony volume.

ALGAL VOLUMES

Table 2.2 indicates ranges of algal volumes and units determined during the present study. It should be noted that the definition of a 'colony' of Microcystis aeruginosa is used only loosely, as such units were frequently multiple, ie aggregations of several colony-sized units connected by a few cells. Such aggregation were most often recorded in very dense populations or 'blooms', but may have been artifacts of preservation. Microcystis 'colonies' over 5 mm in length were recorded on more than one occasion (see also WETZEL, 1975).

Over 1500 different bottle and net samples from openwater cruises were examined and counted during the present investigations and algal volume, frequency and sampling efficiency were accounted for.

A NOTE ON IDENTIFICATION

During the present studies, Planctonema lauterbornii proved to be a characteristic element in the phytoplankton of Lake Turkana. The identification was kindly checked by Professor Bourelly of the Laboratoire de Cryptogamie, Paris. This species was not recorded from the lake by RICH (1933) who noted, however, that Hormidium subtile, a morphologically similar and closely related form, occupied a similar position to P. lauterbornii in the phytoplankton. Since it is unlikely that the populations have changed during the intervening 40 years, it is concluded that the earlier record of H. subtile was a misidentification of P. lauterbornii.

Similarly, while Anabaenopsis is a genus frequently recorded from alkaline East African lakes, and was stated to be common in Ferguson's Gulf in the 1950's (LOWE, 1958), the most frequent heterocystous blue-green alga now occurring in the gulf has unpaired intercalary heterocysts, and is undoubtedly an Anabaena sp.

Algal nomenclature has changed since the Cambridge University Expedition of 1930-31, but it is clear from the present study that the flora of the open water has remained relatively constant in composition over the last four decades, and that sheltered or seasonally enclosed pools now contain very similar algal populations to those reported by RICH (1933).

During the present study, not only the size and shape of algal cells and colonies altered. At times of low algal standing crops, especially away from the Northern Sector, it was noted that colonies of Microcystis aeruginosa varied in cell density within the mucilage sheath, so that a single colony was composed partly of densely packed cells typical of M. aeruginosa and partly of associations of more widely separated cells resembling Synechocystis aquatilis. Such extremes of variation at times affected entire colonies, particularly in regions of the lake away from the influence of the Omo floodwaters.

As a result of this observed morphological variation, colonies which seen in isolation might have been treated as a separate genus were included in the Microcystis group for the purpose of distribution analysis.

THE PHYTOPLANKTON OF THE OPEN LAKE

INTRODUCTION

Floristic changes in the open lake during the period November 1972 to March 1975 are dealt with in this section. Material was collected in the course of joint planktonic/hydrographic cruises described in Chapter 1. Three aspects of the investigations are considered in the sections which follow

(i) algal concentrations

(ii) areal densities

(iii) species composition

In each section, the results are examined in chronological order.

ALGAL CONCENTRATIONS IN THE OPEN LAKE

Algal biomass has been determined for each sampling station by the integration of counts from bottle collections and, whenever possible, from horizontal and vertical net hauls. At some stations, particularly during earlier cruises, these sources were not all available for each station, and in such cases correction factors derived from net and bottle samples at one site, have been used to adjust values at other sites on the same cruise.

The results, showing regional and seasonal variations in algal concentrations, are illustrated in Figures 2.1 to 2.7. Algal concentration, which is expressed in mm^3/litre, is defined as the mean biomass of algae per unit volume of lake water integrated over the entire water column.

Figures 2.1 to 2.7 illustrate not only the distribution of algal biomass within the lake, but also changes through the study period. During November-December 1972 (Fig. 2.1) the River Omo flood water was still in evidence in the Northern Sector, and algal concentrations were high, exceeding 10.3 mm^3/litre (for definition of lake sectors see Fig. 1). Although no data are available for the Central Sector, much lower concentrations were recorded away from the influence of the River Omo in the south with densities reaching a maximum of only 0.25 mm^3/litre. Similar results were obtained in the south in March 1973 (Fig. 2.2) but although concentrations increased to the north, populations had declined noticeably near the main inflow since the previous sampling period.

Samples for June-July 1973 indicated that the population decline had progressed to include all areas of the lake with particularly low concentrations at both the northern and southern extremities (Fig. 2.3). During this period, it is worthy of note that inshore stations generally supported higher algal densities than those situated well away from the shore.

During the main flood season in October 1973, samples from the Central Sector of the lake contained considerable quantities of suspended detritus of Omo origin, as a result of which accurate measurements of algal density were not possible. It was clear, however, that surface concentrations of algae were extremely high during this period in the Northern and Central Sectors, where blooms were frequently noted in the extensive area covered by the sediment plume. In more southerly areas, concentrations were generally greater than in the non-flood season, and values of up to 0.25 mm^3/litre were recorded at several sites (Fig. 2.4).

Results for August 1974 (Fig. 2.5), at the onset of the main flood season, show a similar pattern to that observed in June-July 1973, with relatively low concentrations in most areas. No records are available for the northern extremity of the lake where lowered values were recorded in June-July 1973.

Data for December 1974 covering the Northern and Central Sectors (Fig. 2.6) show a considerable increase in concentrations. As in previous surveys, there was a clear tendency for densities to decrease southwards and the peak value of 8.25 mm^3/litre was recorded in the Northern Sector. Observations for March 1975 indicate that the situation in the Northern and Central Sectors had remained comparatively unchanged, although concentrations of up to 35.6 mm^3/litre recorded in the north were the highest observed during the present series of openwater surveys. As in most previous sampling periods, concentrations were considerably lower in the Southern Sector away from the immediate influence of the River Omo (Fig. 2.7).

Areal densities of algae in the open lake

The results which hitherto have been expressed as biomass per unit volume are now examined in terms of areal density, i.e. biomass per unit surface area quoted in mm^3/m^2. In such units, regional variations in standing crop appear less extreme, since as shown previously, shallower water tended to carry the highest algal concentrations. Modifications to the distributional patterns shown in the concentration charts (Figs. 2.1 to 2.7) are evident and in some cases the reversal of trends is also apparent. Thus in both March 1973 (Fig. 2.9), June and July 1973 (Fig. 2.10) and August 1974 (Fig. 2.12) the highest areal densities were recorded in the Central Sector of the lake. A tendency for algal cover to be particularly concentrated in the Northern Sector was noted only in the late flood and post flood seasons as demonstrated by observations for November-December 1972 (Fig. 2.8), December 1974 (Fig. 2.13) and March 1975 (Fig. 2.14). During the last of these months areal densities had risen to an exceptionally high peak of 783,000 mm^3/m^2 in the Northern Sector which contrasted sharply with a value of only 19 mm^3/m^2 recorded at the most southerly station (Fig. 2.14).

In a number of months, the difference between areal densities in the deep waters of the Southern Sector were relatively slight. During October 1973 (Fig. 2.11), when quantitative results were obtained for only the southern half of the lake, there was a decided tendency for algal cover to increase progressively from Central Island southwards to a peak of 17,600 mm^3/m^2 south of South Island.

DISCUSSION

It is clear that algal density varies seasonally in the lake. From Figures 2.1 to 2.7, results indicate that algal concentrations reach annual maxima between October and March, especially in the Northern and Central Sectors. For the rest of the year, algal biomass was relatively low and more evenly distributed over the lake as a whole.

The flood season of the River Omo has been described in Chapter 1 and from a comparison of results it is clear that there is a direct relationship between flood season and period of greatest algal concentrations, especially in areas closest to the inflow. Records of surface blooms in the Northern and south Central Sectors indicate that large areas of the lake were covered with patches of algae, estimated in some cases to be over 20 km in extent. These blooms, which formed during the calm late morning and afternoon periods, were sometimes blown downwind en bloc, to build up on the western shore. On one such occasion, algal densities at Todenyang reached 1.74 x $10^3 mm^3$/litre and resulted in severe deoxygenation during decomposition, which led to mortality among fish living close inshore. Similar concentrations were recorded in October 1972, 1973 and 1974. Local westerly winds, on occasion, led to blooms building up in the north east corner of the lake in the vicinity of Bani Bay.

In more southerly areas of the lake, the range of algal concentrations was much smaller, and no 'bloom' conditions were encountered. This may have been due partly to stronger winds keeping algae vertically mixed, but also to far lower algal concentrations in the area. Peak densities in the southern basin did appear to rise after October, but higher levels did not persist for so long.

Exceptionally high algal densities were noted in the Northern Sector during March 1975 (Fig. 2.14) suggesting that the influence of the River Omo floods was prolonged well into the dry season. As was reported in the section on physical and chemical limnology (Chapter 1), material carried into the lake by the River Omo spread gradually through the Northern and Central Sectors to influence the Southern Sector. The time which elapsed between flooding and the penetration of riverine water, together with its sediment load, to the southern extremity of the lake is not accurately known since the effect of the River Omo lessened in the lake with distance from the delta. It appears, however, that the influence of flooding in August-September may not have reached the south end of the lake until the following March.

A general tendency for shallower regions to support different algal concentrations is discussed at length below. It is of interest to note that higher algal densities in the Southern Sector were frequently observed off the west coast of South Island and near the east shore in the Loiengalani area. Indications from temperature data (Chapter 1) are that upwelling occurs in such areas, bringing more nutrient-rich water through the column from deep counter-current systems.

SPECIES COMPOSITION OF THE OPENWATER PHYTOPLANKTON

In addition to changes in algal biomass, the species involved fluctuated in dominance and distribution. Figures 2.15 to 2.21 illustrate spatial and temporal changes in the species composition at a series of eight stations situated along the axis of the lake. The concentration of each species is expressed as a percentage of the total concentration of algae recorded for each station during a particular survey. Where an alga forms less than one percent of the total biomass, it has been omitted, although less abundant forms may be of importance as indicator species, as will be discussed below.

It is stressed that the pie diagrams illustrating species composition (Figs. 2.15 to 2.21) do not provide comparisons of biomass between sites. The results should be interpreted in conjunction with the data illustrated in Figs.2.1 to 2.7.

Data for November-December 1972 (Fig. 2.15) during the immediate post-flood period show that Microcystis aeruginosa formed over 93% of the algal volume present at the sampling site in the Northern Sector. Phormidium mucicola and Spirulina laxissima formed a small proportion of the biomass at this site but were numerically important. Raphe-bearing diatoms were generally more important at the three southern stations, forming the bulk of phytoplankton in the Turkwell-Kerio Sector, and occurring co-dominantly with Botryococcus braunii to the north of South Island and with Microcystis spp. at the most southerly station. Surirella spp. were generally the most important diatoms, but in the extreme south other raphe-bearing species were common, including Rhopalodia gracilis, R. gibberula, Gomphocymbella beccari and Nitzschia palea. All of these were common, attached forms in the littoral region of the southern basin, and their presence in the plankton was probably due to wind generated wave action which loosened them from rocks and transported them offshore. Surirella engleri and S. birostrata which occurred commonlynorth of North Island were also of littoral origin.

By March 1973 the influence of the River Omo was declining and algal concentrations had fallen to ca 1.0 mm /litre. Microcystis aeruginosa was again the dominant species in the Northern Sector but was replaced increasingly by Botryococcus braunii further south (Fig. 2.16). Botryococcus braunii thus formed 94% of the biomass in the Turkwell-Kerio Sector but was replaced in turn by Surirella spp. in the extreme south.

The situation had changed considerably by June-July 1973 (Fig. 2.17) with a marked increase in the proportion of Planctonema lauterbornii at all stations to form 40% of the algal biomass of the entire lake. Microcystis spp. and B. braunii were frequent at all stations.

During October 1973 (Fig. 2.18) samples were limited to the southern half of the lake and throughout this area the species composition of the phytoplankton was remarkably uniform, with Microcystis aeruginosa forming between 70% and 83% of the algal biomass and Surirella spp., Botrycoccus braunii and Planctonema lauterbornii comprising the remaining 17-30% in roughly equal proportions.

In August 1974 (Fig. 2.19) with lake levels at a seasonal minimum, B. braunii was dominant in the Northern Sector but became less numerous further south. Microcystis spp. predominated in the Central and Turkwell-Kerio Sectors and Surirella spp., which were common from the region of Central Island southwards, were the most important phytoplankters in the extreme south. Centric diatoms, mainly Coscinodiscus rudolfii, formed an appreciable proportion of the algal biomass in the area to the north of Central Island during this period.

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High algal concentrations were recorded in December 1974 during the post-flood season and Microcystis spp. were the most important phytoplankters with B. braunii subdominant (Fig. 2.20). Planctonema lauterbornii was numerically common throughout the area sampled and formed ca 6% of the biomass south of Central Island. Exceptionally high concentrations were recorded in the Northern Sector of the lake during March 1975 (Fig. 2.21) and Microcystis spp. again predominated in the high density areas. They were replaced, as biomass decreased southwards, by other species. Microcystis spp. thus formed over 90% of the algal biomass in the Northern Sector but only ca 8% in the Southern Sector where diatoms became volumetrically dominant.

CONCLUSIONS

Four main points emerge from the foregoing account of openwater phytoplankton distribution.

(i) Although the climate is stable and temperature/mixing regimes within the lake vary only slightly, marked seasonality exists which dramtically affects the algal community. This may indicate that the populations are unstable, and limited by one or a very few factors which are introduced seasonally by the River Omo flood water.

(ii) A single species of alga, Microcystis aeruginosa, dominates the phytoplankton during periods when the influence of Omo flood water is high, almost to the exclusion of species regularly encountered at other times.

(iii) The species diversity of the openwater is very low, only seven or eight algae forming the bulk of the phytoplankton. Further inshore, and especially in high-energy waters near rocky coastlines, the diversity increases as epibenthic algae - mainly diatoms - are recruited to the plankton.

(iv) Outside the Northern Sector and the Omo flood water influence zone, algal biomass is not high, and mean annual standing crops of planktonic algae are generally very small, particularly in the Southern Sector.

SEASONAL VARIATIONS IN ALGAL VOLUMES AT STATION H1

Samples were obtained from Station H1, situated ca 2 km north of Central Island with a lake depth of over 80 m, throughout the study period. Figures 2.15 to 2.21 indicate that Microcystis dominated the phytoplankton volumetrically in the Central Island area over most of the period, with the exception of March 1973.

Seasonal changes in concentrations of Microcystis at Station H1 are shown in Figure 2.22 which includes data for a total of 24 monthly samples. The mean unit volume of individual Microcystis colonies for each of the samples is plotted in the same figure. The curves follow a similar pattern indicating that larger colonies tended to occur when concentrations of Microcystis were high. The results show that algal concentrations followed a regular seasonal pattern at this typical openwater site. Concentrations rose markedly during the flood season from August onwards, to reach a peak in December, the early post-flood season. Concentrations subsequently decreased to a minimum in May, June and July. The cycle closely follows seasonal fluctuations in lake level and concomitant changes in water transparency and conductivity (see Chapter 1).

No obvious seasonal changes in the colony size of other major phytoplankters was observed.

TRANSVERSE CHANGES IN PHYTOPLANKTON DISTRIBUTION

Data presented earlier in this section illustrate several instances where algal concentrations and areal densities varied from east to west across the lake, in addition to the longitudinal changes under investigation (see Figs. 2.1 to 2.14). A more detailed study of this aspect of distribution was performed on an east-west transect running from Allia Bay to Longech Spit during February 1975, and data from a total of seven sampling stations were obtained (Figs. 2.23-2.25).

Results expressed in terms of algal concentration (Fig. 2.23) show that population levels were generally moderate and tended to fall towards the east shore. Areal densities plotted in Figure 2.24 indicate that algal cover rose considerably in mid-lake where depths exceeded 80 m (Fig. 1). Changes in species composition along the transect are shown in Figure 2.25. Microcystis spp., Botrococcus braunii and raphe-bearing diatoms dominated the phytoplankton volumetrically, while Planctonema lauterbornii was numerically common but of secondary importance in terms of biomass.

The marked changes in species composition along the transect are a reflection of the overall pattern of water circulation in Lake Turkana. It was shown previously that during the post-flood season Microcystis dominated the phytoplankton of the Northern Sector. The preponderance of Microcystis in the eastern half of the transect was correlated with the post-flood movement of water southwards along the eastern shore. Surface currents moving in a north-westerly direction were strongest near the western shore. These currents in turn transported material from the south and were responsible for the greater densities of Botryococcus braunii, Planctonema lauterbornii and *Surirella* spp. on the western side of the transect.

At the two most westerly stations, algae originating from Ferguson's Gulf formed up to 30% of the total biomass. The species concerned, *Anabaena circinalis*. *Spirulina laxissima*, *Cyclotella meneghiniana*, *Stephanodiscus astraea*, *Navicula* spp. and *Nitzschia* spp. were drawn out of the gulf by currents moving along the western shore (see Chapter 1).

PRIMARY PRODUCTIVITY IN THE OPENWATERS

Introduction

The quantification of organic productivity by tropical freshwater phytoplankton is becoming more precise. Recent publications by TALLING *et al* (1973); GANF (1974); MELACK and KILHAM (1974); GANF and HORNE (1975) and MELACK (1976) have extended the validated work in East and Central African lakes.

During the present survey, studies were undertaken to determine oxygen production at sites over the lake at different times of the year, and hence derive a proposed 'average' value for integral daily and annual photosynthesis. Symbols used throughout the discussion are those of WINBERG (1971), and are listed in Table 2.3.

Productivity at Station H1

Vertical profiles of gross oxygen production per unit of lake water are given in Figure 2.26. These represent the extremes of productivity recorded at H1 during 1973. Maximal rates were associated with dense algal cover in January of that year (see Fig. 2.22), and minima with the lowest densities in June. Values of A_{max} were 684 mgO$_2$/m^3/hr in June.

Lakewide observation of open water productivities

From Figures 2.8 to 2.14 it is clear that algal density varies greatly with site and season in the open lake. It was therefore reasonable to expect that algal productivity rates would similarly exhibit wide ranges from cruise to cruise. Figure 2.27 illustrates values of A_{max} recorded along the axis of the lake during times of lowest algal densities, during June and July 1973. A 10-fold difference exists between the lowest photosynthetic rates, west of South Island, and the highest in the middle of the Northern Sector.

By constrast, the extended rectangular cruise in December 1974 (Fig. 2.28) provided data for the Northern and Central Sectors at a time of increasing algal densities. Maximum rates, up to 540 mgO$_2$/m^3/hr were recorded in the Northern Sector.

Three months later, in March 1975, when the highest algal densities were recorded, (Fig. 2.7), a 100-fold variation in production rates from the Northern to the Southern Sectors was observed (Fig. 2.29).

Integral photosynthesis in the open water

When primary productivity values were determined on an areal basis, similar ranges between sites and times was recorded, but the variation was less since lower algal concentrations tended to occur in clearer waters where the euphotic zone was deeper. Figure 2.30 shows values of A from the lake during June and July. Rates were between 75 $mgO_2/m^2/hr$ in the south, and 380 $mgO_2/m^2/hr$ in the north.

Areal production in December (Fig. 2.31) was considerably greater than in June-July, but lower than in March 1975 (Fig. 2.32) when values ranged from 85 $mgO_2/m^2/hr$ in the Southern Sector, to over 1800 mgO /m /hr in the middle of the Northern Sector.

Review of open water productivity results

The present studies have shown that for most of the lake mean algal concentrations were low for much of the year. Productivity measurements have proved that seasonal trends in population densities were paralleled by changes in A_{max}. However, values of A_{max} were rather higher than would be expected if algae were distributed more evenly throughout the water column by continuous mixing currents.

Frequently, calmer periods during afternoons and evenings led to the upward movement of algae in relatively calm water. Such tendencies are discernable in observations of the vertical distribution of phytoplankton at Station H1 during a 24 hour station (Figs. 2.33 to 2.35). The algae concerned, Botryococcus braunii, Microcystis spp. and Planctonema lauterbornii comprised over 85% of the algal biomass. Most primary productivity investigations were performed during the early afternoon, and it is clear that at this time, ca 50% of the algal populations normally lay within the upper 15 m of the water column. High winds in the early morning generally resulted in a breakdown of algal stratification, and precluded in situ enclosure incubation of lake water. The range of integral photosynthetic production at H1, from ca 635 to 1140 mgO /m /hr, was thus higher than would be expected from evenly distributed phytoplankton.

One of the basic assumptions for the application of Talling's model for integral photosynthesis per unit area (TALLING, 1965) is that algae are homogeneous within the photosynthetic zone. Variations in the depth of the euphotic zone in the distribution of algae and in radiation were generally large in Lake Turkana, and the model is generally not applicable. However, the model predicts, fairly closely, integral rates for the curves shown in Figure 2.26. Minimal calculated rates of 708 $mgO_2/m^2/hr$ compare with planimetric integration values of 635 $mgO_2/m^2/hr$, while maximal rates are predicted to be 1360 $mgO_2/m^2/hr$.

The Omo flood water brings large quantities of suspended solids into the lake as illustrated by the E R T S photographs reproduced in Chapter 1 (Plate 1.12). This material reduces light penetration and shifts the A ϵ depth upwards. Similarly, ϵ min generally lies within the green spectral region for much of the clearer areas of the lake (Chapter 1) but is shifted towards the red region by high densities of suspended particles. In the offshore waters of Lake Victoria ϵ min remains within the green waveband, and light penetration varies mostly with changes in algal densities, not with the import of allochthonous solids (TALLING, 1965).

The model works satisfactorily for deep euphotic zones, eg Lake Victoria, as well as for shallow euphotic zones, eg Lake George, when the condition of homogeneous phytoplankton distribution is fulfilled (see also GANF and HORNE, 1975).

When A_{max}/ϵ_{min} ratios are plotted against integrated or predicted values from Figure 2.26, the points fall within Talling's boundary lines (Fig. 8a, p 22 of TALLING, 1965).

THE PHYTOPLANKTON OF FERGUSON'S GULF

INTRODUCTION

As has been mentioned previously (page 18), shallow inshore areas protected from the continual mixing effects of deep offshore currents develop algal floras which are very different from those of the open water of the lake. Currently, the largest such inshore area is Ferguson's Gulf (see Chapter 1, page 11). With an area of ca 35 km the gulf maintains a dense permanent standing crop of phytoplankton, varying in density more with site and time of day than with season.

PREVIOUS RECORDS

RICH (1933) notes that the dominant algae of the gulf were *Hormidium subtile*, *Phormidium molle* and *Cyclotella meneghiniana* with *Botryococcus braunii* becoming more numerous towards the northern end in the vicinity of the mouth. BEADLE (pers. comm.), who was a member of the Cambridge expedition, recalls that the gulf was then (1930-31) a bright green colour, suggesting that the water body was physically and floristically intermediate between the openwater and inshore types (see Chapter 1, pages 11 to 12 for a description of physical changes in the gulf since the Cambridge expedition).

RICH (*op. cit.*) also states that smaller, enclosed, alkaline pools on Longech Spit had dense populations of *Spirulina platensis*, with *Anabaenopsis*, *Kirchneriella* and *Crucigenia* spp., algae closely related to currently dominant forms and similar to those found in such pools during the present study.

LOWE (1958) observes that the stomachs of *Sarotherodon niloticus*, which during the present study proved to be a fairly unselective phytoplanktophagous fish (see pages 1362-1365) were full of blue-green algae, notably *Spirulina* and *Anabaenopsis* spp. These results prove that the two algal genera were not restricted to enclosed pools during the 1950's.

TRENCH (1966) includes colour plates of Ferguson's Gulf which leave no doubt that a very dense algal flora was present about ten years before the start of this study.

THE CONTEMPORARY FLORA

During the present investigations, the phytoplankton of Ferguson's Gulf was dominated numerically and volumetrically by blue-green algae, and greater importance is given here to algal volumes (or biomass) than to frequency. Figure 2.36 illustrates algal biomass at ten stations in Ferguson's Gulf during April 1975. The major phytoplankters are noted in Table 2.4.

As was shown in Chapter 1, mid-morning winds mixed the water thoroughly from top to bottom and samples described here were collected from sub-surface (ca 15 cm) water during such conditions. Mean algal counts from the ten sites are presented in Table 2.4. The densest algal concentrations were recorded at Sites 3, 7 and 8 (Table 2.5) on the eastern side of the gulf. Filamentous blue-green algae were dominant in terms of biomass at all stations and formed from 52%-92% of the total. The most important species was Anabaena circinalis which contributed between 47% to 86% of the total biomass. Coccoid blue-green algae and diatoms, especially Nitzschia spp. formed most of the remaining biomass except at Sites 3, 7 and 10, where green algae were locally important. Botryococcus braunii was the dominant green alga and formed over 95% of the biomass of this group.

Wind-driven water movement from the open lake around the northern tip of Longech Spit and into Ferguson's Gulf has been reported in Chapter 1 (see page 18), and further evidence has been provided by the distribution patterns of algal species. Thus, Botryococcus braunii was a common phytoplankter in the open lake in the region of Longech Spit during the April 1975 survey of Ferguson's Gulf. The results suggest that currents of relatively low conductivity water carried B. braunii and other open water algae into the gulf where they persisted at higher conductivities in the vicinity of Sites 3, 7 and 10.

Other green algae and the dinoflagellate Gymnodinium aeruginosum were more frequent in shallow water at the margin of the gulf where most of the raphe-bearing diatoms originated. Although Anomoneis, Nitzschia and Rhopalodia spp. were most commonly found attached to the sand or mud at the very edge of the gulf, they were removed from this epibenthic state and suspended in the gulf by wind-driven currents. Rhopalodia gracilis was most abundant at Site 7, while Anomoneis sphaerophora and Nitzschia spp. were more abundant to the northwest.

HORIZONTAL WATER MOVEMENT

Abrupt changes of water colour were observed in Ferguson's Gulf both at the mouth and within the embayment (see Chapter 1, Plate 1.2). The main body of gulf water was bright green. Gulf water, clearly distinguishable by its colour, at times extended in a narrow inshore strip up the west coast beyond Nachakui, (page 49), a distance of over 60 km. This movement resulted both from direct wind action and from the incursion of lake water into the north eastern area around the tip of Ferguson's Spit.

From Table 2.5, it can be seen that Station 7 supported not only the greatest biomass of algae, but also the highest chlorophyll a: algal volume ratio, over 7 $\mu g/mm^3$. Values for Site 5 in the southwest corner show that both biomass and ratio were lower. These results indicate less favourable conditions for algal growth in the south and west of the gulf. The water in these shallow areas was muddy-brown in colour and contained suspended solids stirred up from the loose sediments by wind action.

It is likely that the higher chlorophyll a concentrations at Sites 3, 7 and 8 were due to upwelling of nutrient-rich water along the inside of the spit. The movement of water across the surface of the gulf by the south-easterly winds would tend to create a counter-current system bringing water from deeper layers to the surface in the southeast corner.

Investigations of the biology of Sarotherodon spp. (see Chapter 8 page 1348) show that the east and south east regions of Ferguson's Gulf were important areas for breeding and nest-building. A high proportion of the fish caught by commercial fishermen in this area were, however, immature and feeding actively. Denser algal populations in the south and east may be a further critical factor governing their distribution.

Evidence that food was available for Sarotherodon spp. in the gulf prior to the explosion of the fishery in 1975, is given in Table 2.6 where spasmodic algal counts and biomass determinations carried out between October 1972 and June 1975 are presented.

PHOTOSYNTHESIS AND COMMUNITY RESPIRATION IN FERGUSON'S GULF

From Figure 1. (see Chapter 1) it is evident that stratification rapidly builds up after cessation of the strong south-easterly winds. Several early morning records from Ferguson's Gulf suggest a dawn oxygen content of 8.9 mgO_2/litre (ca 116%) throughout the water column. High photosynthetic rates, coupled with total mixing conditions persist and maintain super-saturated oxygen concentrations up to 10.2 mgO_2 /litre (ca 135%) before the wind drops, but subsequent community respiration rapidly depletes the oxygen reserves below the euphotic zone.

Gross photosynthesis in tropical lakes has been estimated by diurnal changes of dissolved oxygen in situ. Recent studies include those by TALLING et al (1973); MELACK and KILHAM (1974) and GANF and HORNE (1975). By accepting the method of GANF and HORNE (1975) and applying it to Ferguson's Gulf, estimates of gross production have been achieved. Calculations involve planimetric integrations of total dissolved oxygen during daylight hours, and estimates of net increase rates per unit area together with community consumption rates in deeper waters affected by depletion during calm afternoon stratification. This method does not take into account diffusion rates or variations in respiration. Variables accounting for oxygen loss to the air were not included in this simplistic approach since no reliable wind speed records are available for the sampling period.

However, from six integrations of oxygen content per unit area, a maximal post-dawn increase from 16.0 to 22.5 gO_2/m^2 was recorded. The mean change in dissolved oxygen concentration at depths greater than 100 cm (but above the substrate) was calculated to be 233 mgO_2/m^3 /hr. Assuming this community respiration rate to be constant, the integrated value becomes 419 mgO_2/m^2/hr, or 5.03 gO_2/m^2/12 hrs. Thus the gross production is (22.5 - 16.0) 6.5 gO_2/m^2 (minimum column net oxygen production for daylight hours) plus 5.03 gO_2/m^2 (community respiration rate for 12 hours) which equals 11.53 gO_2/m^2/12 hrs.

Severe limitations must be attached to this method. Ferguson's Gulf is subjected to strong winds, particularly during the morning hours (Fig. 1.38), which complicate estimates of diffusion rates and, indirectly, reduction of column oxygen content by mixing with the highly reduced, flocculent, organically rich sediments. Such short comings tend to produce underestimates of gross production by this method, but it is accepted that the use of in situ oxygen production and consumption calculations often give more realistic estimates than enclosed techniques, especially in waters with dense algal populations (MELACK and KILHAM, 1974).

It is suggested that the simplicity of the acetylene-reduction technique and its use as a field assay method make it ideal for further studies on Lake Turkana, provided that an acetylene-ethylene gas analysis instrument (Gas-Liquid Chromatograph) is accessible within a few days of the field trials.

LITTORAL ALGAE

ALGAL DISTRIBUTION IN THE LITTORAL REGION

During the present study, over 110 different algal species (Table 2.8) were recorded from littoral habitats in Lake Turkana. Most data were obtained from samples collected during the shore survey (see Chapter 7) and Figure 2.37 a-c illustrates the frequency of taxa noted during these investigations in different areas of the lake. Data from groups of stations have been combined for the sake of clarity, to provide a summary of the algal flora of sections of coastline ranging from ca 10-20 km.

Although fine net samples on which the shore survey was based provided chiefly quantitative assessments of the flora, some indications of algal abundance also emerged. There was a general tendency for the number of individuals to rise with the number of taxa.

Phylum Chrysophyta

The Chrysophyta was represented solely by diatom species in the shore samples, and formed the largest littoral algal group, both in the numbers of taxa and of individuals. Figure 2.37a shows that the numbers of diatom species rose from two on high energy shorelines with unstable substrates, such as the west coast north of Longech, to 28 in very sheltered habitats providing a range of stable substrate types, as for example El Molo Bay.

Certain diatom populations, dominated by specific associations, were recorded in similar habitats around the lake. Rather exposed shores in the north-eastern corner were dominated by inshore communities of *Coscinodiscus rudolfii* and attached colonies of *Caloneis aequatorialis*, *Nitzschia granulata* and *N. palea*. Further south, exposed shores to the east of the lake frequently supported dense, almost uni-algal crops of *Gomphocymbella beccari*, especially in very shallow rocky bays.

By contrast, sheltered bays in the northeast supported large populations of *Rhopalodia gibba*, *R. gracilis* and *R. vermicularis*. These were supplemented in bays with sandy or rocky substrates by *G. beccari*, *Surirella* spp. and, in muddy bays, by centric diatoms, notably *Stephanodiscus astraea* and *Cyclotella meneghiniana*. Among macrophyte stands in Allia Bay *C. meneghiniana* became very numerous, with densities of over 2500 cells/ml in unconcentrated samples. Away from the densest macrophyte stands, *Anomoneis sphaerophora*, *Cumbella mulleri*, *Nitzschia epiphyticoides* and *N. palea* were also common.

Sheltered areas of the west shore, for example Meriar and Lolibekai, sustained diatom associations typical of muddy substrates and macrophyte stands, although *Stephanodiscus astraea* was less frequent. *Rhopalodia gibberula*, *R. gracilis* and *Surirella fulleborni* dominated the populations, which also included *Anomoneis sphaerophora*, *Cymbella mulleri*, *Navicula pupula*, *Nitzschia palea* and *N. punctata*.

More exposed western shores of mobile gravel or sand supported poor algal communities, mostly of *Cocconeis placentula*, *Achnanthes exigua* and *Rhopalodia gracilis*, with *Nitzschia bacata*. An exception to this generalisation was an outcrop of soft sedimentary rock north of Audache, where firmer substrate permitted a more diverse diatom population to exist, including *Anomoneis sphaerophora*, *Cymbella muller*, *Navicula cryptocephala* and *Rhopalodia* spp. (see Fig. 1. Shore features).

Phylum Cyanophyta

The second longest taxonomic group was the Phylum Cyanophyta or blue-green algae. The number of blue-green algal taxa in littoral habitats nowhere exceeded nine. It must be remembered, however, that the shore samples were collected from the margin of the lake and that, as shown previously, large sheltered water bodies developed characteristic algal florae (see Table 2.8). Some sites sampled were isolated lagoons where dense but almost uni-algal blue-green populations may persist. In Audache lagoon *Spirulina platensis* populations persited from 1972 to 1974 colouring the water a deep pea-green.

Figure 2.37b shows the frequency of blue-green algal taxa around the lake shore. As with diatoms, more sheltered waters with a range of habitat types, generally supported larger numbers of species. It is evident from Figure 2.37b that fewer species were recorded in the Southern Sector than elsewhere, even in sheltered bays. On low energy shores the species recorded included *Anabaena circinalis*, *Anabaenopsis arnoldii*, *Spirulina laxissima* and *S. plantensis*. Attached algae, notably *Calothrix* spp. which grow periphytically in sheltered habitats, were occasionally recorded loosened in the littoral plankton.

Microcystis spp. were frequently recorded during the shore survey but it seems likely that they were transported into the littoral region by wind action and originated elsewhere.

Phylum Chlorophyta

The green algae, Phylum Chlorophyta, were represented by up to four taxa at one site and were clearly defined in habitat type (Fig. 2.37c). Sheltered bays supported sparse colonies of attached algae, *Oedogonium*, *Spirogyra* and *Stigeoclonium*, as well as certain planktonic types, *Cosmarium* sp. *Scenedesmus quadricauda*, *Schroederia setigera*, *Staurastrum* sp. and *Tetrastrum heteracanthum*. Of these, *Scenedesmus* and *Tetrastrum* were most frequently recorded. *Botryococcus braunii* and *Planctonema lauterbornii* were also found in the littoral region but, as in the case of *Microcystis* spp., these open water forms were probably transported into shallow water by wind generated currents.

Phylum Pyrrophyta

Only *Gymnodinium aeruginosum* was recorded in the littoral zone. The species also occurred in shallow water in sheltered bays.

Table 2.8 summarises the algal species recorded from littoral samples during the present study, and indicates their probable habitat of origin. It should be noted that several forms of the genus *Nitzschia* were recorded which did not fit descriptions in the literature cited in the bibliography.

LITTORAL PRODUCTIVITY

Introduction

As mentioned previously, algal material commonly became detached from the shoreline, especially in the Southern Sector, and was transported into the plankton by wind-driven waves and currents. The material usually originated as part of the rich 'Aufwuchs' community on the more sheltered, west-facing coasts, and contributed greatly to the plankton biomass.

Attached algal communities in the southern basin were mainly epilithic or episammic and were at times very dense. Species diversity was frequently high but the genera *Cymbella*, *Comphocymbella*, *Nitzschia* and *Rhopalodia* regularly dominated the associations. Large stretches of shoreline were covered by a unialgal flora - as was the case on the rocky shoreline south of Loiengalani, where *Gomphocymbella beccari* predominated.

Experimental determination of littoral primary productivity

Using light and dark bottle techniques with flasks and perspex tubes, and gaseous oxygen capture, estimates of gross productivity by suspended and attached littoral communities have been made.

Table 2.9 summarises results from three sites in the Southern Sector including estimates of macrophyte (*Potamogeton pectinatus*) productivity by oxygen production. The times shown indicate when the field work was carried out and do not represent incubation periods, which were generally between 60 and 80 minutes. Values per unit area for attached algae production have been corrected for production by suspended material within the enclosure. Corrections have also been applied to macrophyte data to allow for differences between the light and dark tubes in the dry weights of plant material incubated.

Production estimates obtained with inverted flasks varied both with time of day and site. The differences between production levels recorded on El Molo Island (Site A) and the shore of El Molo Bay (Site B) is explained chiefly by variations in biomass. During June 1975 the lake level was approaching its seasonal minimum and had tended to stabilize. Epilithic algae at Site A were well-developed and the area enclosed was ca 30 cm below the lake surface. Dense algal communities, mainly of *Gomphocymbella beccari*, were recorded from stones removed for later examination. The surface area of substrate covered by the flask considerably exceeded the plan area covered by the flask (46.6 cm) since it was composed mainly of small stones from 1-3 cm diameter.

Site B was on a ridge of coarse sandy-gravel which was covered to a depth of only ca 15 cm by lake water. Episammic algal communities produced a fine mucilaginous covering, binding the substrate surface, not a dense algal coat as was noted at Site A. The main algal species present were *Surirella biseriata*, *S. engleri* and *Rhopalodia vermicularis*. Production rates at Site A were 37% greater than at Site B (Table 2.9).

Oxygen production associated with epilithic algae at Site C, on the west shore of South Island, indicates that primary productivity was higher than at Site A in El Molo Bay. Variation was also noted at South Island between observations made at different times of the day, with higher values obtained for the earlier sample. It is not possible to quantify production on a unit algal basis, which would have enabled sites to be compared directly, but Site C was in most respects similar to Site A. The midday and mid-afternoon assays at Site C were carried out on the same spot with as little disruption as possible between runs.

Production by suspended algal material (Planktonic production, Table 2.9), over the sites used for benthic production assays, varied from 213 mg $O_2/m^3/hr$ to 367 mg $O_2/m^3/hr$, and on an areal basis, from 64 mg $O_2/m^2/hr$ to 110 mg $O_2/m^2/hr$ over a depth of 30 cm. Total littoral production during the midday period at Sites A and C was between 80 mg $O_2/m^2/hr$ and 130 mg $O_2/m^2/hr$ in water 30 cm deep.

The macrophytes used in the experimental enclosures carried attached algal populations and were surrounded by suspended or truly planktonic forms. No attempt was made to separaate epiphytic, planktonic or macrophytic production. Thus for macrophytes, productivity per unit area and per unit plant dry-weight were assessed to give an integrated estimate for the community as a whole, over the entire water column from substrate to surface. Lacunal oxygen concentrations in macrophytes were assumed to be saturated by midday, so that all oxygen produced could be traced either in solution or as gas evolved from the plants and collected in the tube.

There is a possibility that macrophyte material in the dark tubes may have respired appreciable quantities of lacunal oxygen. Under these circumstances the relatively small changes in dissolved oxygen around the plant would result in an underestimate of productivity. Despite such shortcomings, it is considered that the results are valid and that the gross production rates are typical of Potamogeton in Lake Turkana.

At experimental Site B in El Molo Bay plants of Potamogeton were erect but completely submerged in ca 35 cm of water. The substrate was dense, anoxic mud containing obvious sulphide deposits. The results (Table 2.9) show that areal production rates in the macrophyte beds was from 250% to 420% higher than values for combined benthic plus planktonic algal communities at Sites A and C.

A SYNOPSIS OF PRIMARY PRODUCTION RESULTS FROM LAKE TURKANA

Ranges of gross productivity rates recorded from various regions in the lake are given in Table 2.10. Values are shown as $mgC/m^2/day$, assuming a daily:hourly ratio of 9.2 (derived from figures for Lake George, Uganda, in GANF and HORNE 1975) and a photosynthetic quotient of 1.0.

The most striking features for these values concerns spatial variation and seasonality. As shown above, the phytoplankton varies seasonally in association with flooding cyles of the River Omo. The affects of these cycles on algal populations diminish with distance from the Omo Delta leading to wide ranges in production estimates both within and between lake sectors. The Northern Sector supported denser phytoplankton populations, and consequently higher productivity rates from season to season, than sectors further south.

When considering the relatively low rates of total littoral-algal production against open-water rates, it must be remembered that the water depths concerned were ca 30 cm, and that under such circumstances photo-inhibition of productivity may have occurred. Nevertheless, daily areal production is greater in the littoral than in the open-water of the Southern Sector, and must account for a substantial organic input to that Sector.

Production in macrophyte stands is far higher than in littoral algal associations and would indicate how important as organic sources *Potamogeton pectinatus* beds are to Lake Turkana. Since these beds persist during changes in the lake level by fresh growth in optimal water depths, it may be assumed that such high rates were maintained throughout the year.

In a similar way, the investigations have indicated that the dense planktonic populations in Ferguson's Gulf persist from season to season and that the high production rates in the gulf fluctuate only slightly during the course of the year.

BEADLE (1974) reviews several reports of primary productivity for African waters (pp 104-105, Table 7.1), from which it is clear that the open-water rates recorded here for Lake Turkana are frequently lower than in other deep lakes. The estimates provided in Table 2.10 indicate that total carbon production in Lake Turkana was of the order of 5×10^6 tonnes per year.

SUMMARY

Investigations were carried out on spatial and temporal variations in the algal flora and primary production of Lake Turkana. The open-water species diversity was very low, with *Microcystis* spp. generally dominating the algal biomass, in association with *Planctonema lauterbornii* and *Botryococcus braunii*.

Algal concentrations and primary production rates in the open-water were highest in the Northern Sector, and ranged most widely in the North and Central Sectors. Biomass was generally ver low over the main lake, but concentrations increased during and soon after the River Omo flooded. It is deduced that the Omo supplies some combined nitrogen to the lake, which is otherwise limiting to algal growth.

Dense, inshore phytoplankton populations are maintained in shallow, sheltered regions such as Ferguson's Gulf. Such associations are frequently dominated by heterocystous blue-green algae, for example *Anabaena circinalis*, which in turn support large populations of the commercially important cichlid *Sarotherodon niloticus*.

The high organic production rates of such inshore regions probably represent important sources of material for open water areas. Productivity in littoral zones was associated mainly with epibenthic diatoms, and in the Southern Sector, areal production in such communities was much higher than planktonic production in the open lake.

Sheltered bays supported dense stands of *Potamogeton pectinatus* which, in association with epiphytic algae, produced oxygen at similar areal rates to those recorded in Ferguson's Gulf. The macrophytes must therefore be regarded as an important source of organic input to the lake as a whole.

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TABLE 2.1

Algal species reported from Lake Turkana by previous workers

RICH (1933)

Open-water forms

- *Hormidium subtile*
- *Botryococcus braunii*
- *Microcystis flos-aquae*
- Diatoms

Ferguson's Gulf

- *Hormidium subtile*
- *Phormidium molle*
- *Cyclotella meneghiniana*
- *Botryococcus braunii*
- Diatoms

On macrophytes around Ferguson's Gulf

- *Lyngbya lutea*
- *Nostoc* sp.
- *Calothrix* sp.
- *Rhopalodia gracilis*
- Diatoms

In enclosed pools

- *Arthrospira platensis*
- *A. platensis* forma *minor*
- *Hormidium subtile*
- *Anabaenopsis arnoldii*
- *Kirchneriella lunaris*
- *Crucigenia quadricauda*

Central Island, Crater lake A

- *Hormidium subtile*
- *Calothrix* sp.
- *Lyngbya lutea*
- *Rhopalodia gibberula*
- *Rivularia biasolettiana*
- *Surirella biseriata* var. *lanceolata*

Central Island, Crater lake B

Arthrospira platensis

Central Island, Crater lake C

Arthrospira platensis

On macrophytes in Crater lake C

Rhopalodia hirudini formis
R. ventricosa
R. gracilis
R. gibberula var. *rupestris* forma *crassa*
Cymbella grossestriata var. *obtusiscula*
C. helvetica
Gomphocymbella bruni
Gomphonema intricatum
Cyclotella meneghiniana
Navicula pupula
N. sphaerophora var. *rostrata*
N. cryptocephala
N. hungarica

In stomach of *Clarias* sp., mainlake shore of Central Island

Phormidium autumnale
Gomphocymbella bruni
Rhopalodia gracilis
Gomphonema sp.

Algae are listed by RICH (1933) in order of decreasing abundance.

BACHMANN (1938)

Hormidium subtile
Rhopalodia gracilis
R. vermicularis
R. vermicularis f. *perlonga*
Coscinodiscus rudolfii
Cyclotella meneghiniana
Nitzschia palea
Navicula placentula var. *lanceolata*
Cymbella lanceolata
C. maculata
Anomoneis sphaerophora
Surirella biseriata var. *lanceolata*
Gomphonema intricatum

TABLE 2.2

Typical volumes and units of the more common planktonic algae, measured directly.

Alga	Volume um^3	Unit
Anabaena circinalis	3100	coil
Chroococcus minutus	30	cell
C. turgidus	85	pairs
Dactylococcopsis raphidiodes	25	cell
Merismopaedia minima	20	colony
Microcystis aeruginosa	800,000 - 4,000,000	colony
M. flos-aquae	20,000	colony
Oscillatoria curviceps	280	filament
O. schultzii	740	coil
Spirulina laxissima	15	filament
S. platensis	3000	coil
Synechocystis aquatilis	400 - 1500	colony
Anomoneis sphaerophora	1000 - 3000	cell
Coscinodiscus rudolfii	4000 - 8000	cell
Cyclotella meneghiniana	1000 - 3000	cell
Gomphocymbella beccari	2400	cell
Melosira granulata	50,000	filament
Navicula pupula	900 - 1800	cell
Nitzschia epilliptica	90 - 190	cell
N. granulata	200 - 350	cell
N. palea	200 - 600	cell
N. spiculum	100 - 160	cell
Rhopalodia gracilis	12,000 - 47,000	cell
Stephanodiscus astraea	2000	cell
S. hantzschii	200	cell
Surirella birostrata	45,000 - 110,000	cell
S. engleri	60,000 - 150,000	cell
Botryococcus braunii	10,000 - 110,000	colony
Planctonema lauterbornii	450	cell
Scenedesmus quadricauda	800 - 1500	colony
Schroederia setigera	50 - 120	cell
Tetrastrum heteracanthum	580	colony

TABLE 2.3

Symbols used in productivity descriptions

Z_{eu}	depth of euphotic zone, in m
ϵ	vertical extinction coefficient, in ln units/m
ϵ_{min}	minimum value, over spectrum, for
B	population density, in mg/chlorophyll *a*/m^3
A	rate of gross photosynthesis per unit water volume
A_{max}	value for A at light saturation
ΣB	population content per unit area, within the euphotic zone, in mg chl-*a*/m^2
ΣA	hourly rate of gross photosynthesis per unit area (g O_2/m^2/hr)
$\Sigma\Sigma A$	daily rate of gross photosynthesis per unit area (g O_2/m^2/12 h)
P	specific rate of gross photosynthesis per unit biomass (mg/mg chl *a* h)
I_o	irradiance on the water surface
I'_o	irradiance immediately below the water surface
I_k	irradiance indicating onset of light-saturation of photosynthesis (Talling, 1957)

TABLE 2.4

Mean algal counts per 0.1 ml from 10 sites in Ferguson's Gulf: May, 1975

Group		Units
Filamentous Blue-greens		
Anabaena circinalis	1,196	Coil
Dactylococcopis raphidiodides	33	Cell
Oscillatoria curviceps	1,101	Filament
Oscillatoria schultzii	282	Filament
Spirulina laxissima	14,535	Filament
Spirulina platensis	5	Coil
Coccoid Blue-greens		
Chroococcus minutus	11,544	Cell
Chroococcus turgidus	1,698	Pairs
Merismopedia puntata	139	Colony
Diatoms		
Anomoneis sphaerophora	27	Cell
Cyclotella meneghiniana	35	Cell
Navicula pupula	42	Cell
Nitzschia aequalis	1,295	Cell
Nitzschia frustulum	35	Cell
Rhopalodia gracilis	5	Cell
Pyrrophytes		
Gymnodinium aeruginosum	10	Cell
Greens		
Botryococcus braunii	10	Colony
Scenedesmus quadricauda	4	Tetrad
Tetrastrum heteracanthum	148	Tetrad

TABLE 2.5

Algal volumes and chlorophyll a concentrations observed at 10 Sites in Ferguson's Gulf during April , 1975.

Site	Algal volume mm^3/litre	Chlorophyll a mg/m^3	Chlorophyll a /cell volume $\mu g/mm^3$
1	63.9	342	5.35
2	15.2	96	6.3
3	48.2	559	5.7
4	27.8	150	5.4
5	51.4	247	4.8
6	41.9	267	6.4
7	117.4	841	7.2
8	82.1	521	6.4
9	51.4	283	5.5
10	75.3	459	6.1

TABLE 2.6

Algal biomass estimates from Fergusons' Gulf during the present study. All samples were obtained from the subsurface layers at a depth of ca 15 cm during periods when the water was thoroughly mixed.

Site	Date	Chlorophyll a $\mu g/mm^3$	Total volumes mm^3/litre
Jetty	16.11.72	n a	13.95
Mid-Gulf	16.11.72	n a	57.8
Jetty	16. 6.74	205	38.4
Mid-Gulf	16. 6.74	398	108.8
S W Gulf	6. 7.74	n a	131.7
S E Gulf	6. 7.74	n a	111.8
N E Gulf	6. 7.74	n a	12.8
Mid-Gulf	6. 7.74	n a	166.07
Jetty	21. 4.75	150	27.8
Mid-Gulf	21. 4.75	459	75.3

TABLE 2.7

Comparative physical and production data from shallow African waters

Water body	Mean depth (m)	Temperature (°C)	pH	ε min (ln/m)	$\underline{Z}_{eu}$ (cm)	$\underline{B}$ (mg/m^3)	$\sum \underline{B}$ (mg/m^2)	Total cover (mg/m^2)	$\sum \underline{A}$ (gO_2/m^2/hr)	$\sum\sum \underline{A}$ Gross O_2 Production (gO_2/m^2/12h)
Ferguson's Gulf, Lake Turkana	1.8	27.5-32.5	9.3- 9.7	8.6	42-5	376	133	450		11.53
Lake George, Uganda (1)	2.5	26.0-36.0	8.9- 9.7	4.1- 7.7	48-91	125-340	95-217	490	1.68	12.0
Lake Nakuru, Kenya (2)	2.0	21.0-27.0	10.5	10	37	200-910			0.5 - 0.8	36.0
Lake Kilotes, Ethiopia (3)	2.6	18.8-22.5	9.6	7.6-15.4	24-49	205-412	49-194	320-9000	0.47 - 2.4	10.7-12.6
Lake Aranguadi, Ethiopia (3)	18.5	19.7-27.0	10.2-10.6	13.7-24.7	15-27	917-2170	221-325	10000-20000	1.43 - 2.56	43.0-57.0
Lake Chad Chad (4)	3.9	23.0-29.0	8.2						0.79	1.9-7.7

References:
(1) Ganf (1974); Ganf and Horne (1975)
(2) Melack and Kilham (1974); Melack (1976)
(3) Prosser et al. (1968); Talling et al. (1973)
(4) Maglione (1969); Lemoalle (1969, 1973)

TABLE 2.8

Algal species noted in the littoral region during the present study, 1972-1975, with a key to the habitat or origin : a) openwater plankton, b) littoral plankton, c) periphyton.

Chrysophyta	Habitat		
Achnanthes exigua	-	b	c
Amphora ovalis	-	b	c
Anomoneis sphaerophora	a	b	c
Asterionella formosa	-	b	-
Caloneis aequatorialis	-	b	c
Cocconeis placentula	-	b	c
Coscinodiscus rudolfii	a	b	-
Cyclotella comta	a	b	-
C. meneghiniana	a	b	-
Cymatopleura solea	a	b	c
Cymbella lanceolata	-	-	c
C. mulleri	-	b	c
Diploneis (?ovalis)	-	b	c
Fragilaria construens	-	b	-
F. crotonensis	-	b	-
F. intermedia	-	b	c
F. virescens	-	b	c
Gomphocymbella beccari	-	-	c
Gomphonema aequatorialis	-	b	c
Hantzschia amphyoxis	-	b	c
Melosira distans	a	b	-
M. granulata	a	b	-
M. italica	a	b	-
Meridion circulare	-	b	-
Navicula cryptocephala	a	b	c
N. decussus	-	b	-
N. exiguiformis	-	b	c
N. insociabilis	-	b	c
N. menisculus	-	b	c
N. perventralis	-	b	c
N. pupula	-	b	c
N. radiosa	-	b	-
N. severascens	-	b	c
N. subcostulata	-	b	c
N. submollesta	-	b	c
N. tuscula	-	b	c
*Nitzschia adapta	-	b	c
N. aequalis	a	b	c
N. apiculata	a	b	-
N. asterionelloides	-	b	-
N. bacata	-	b	c
N. elliptica	-	b	c
N. epiphyticoides	-	-	c
N. fontinicola	-	b	c
N. frustulum	-	b	c
N. granulata	a	b	c
N. hungarica	-	b	c
N. palea	-	b	c
N. perspicula	a	b	c
N. punctata	-	b	c
N. spiculum	a	b	-
N. subcommunis	-	b	-
Rhopalodia gibba	-	-	c
R. gibberula	-	-	c
R. gracilis	-	b	c
R. hiruduniformis	-	-	c
R. ventricosa	-	-	c
R. vermicularis	-	-	c
Stephanodiscus astraea	a	b	-
Surirella birostrata	a	b	-
S. biseriata	a	b	-
S. constricta	a	b	-
S. engleri	a	b	-
S. fontinicola	-	b	c
S. fulleborni	-	b	c
S. ovalis	-	b	c
S. ovulum	-	b	c
Chlorophyta			
Botryococus brauni	a	-	-
Cosmarium sp.	-	b	-
Oedogonium sp.	-	-	c
Planctonema lauterbornii	a	-	-
Scenedesmus quadricauda	-	b	-
Schroederia setigera	-	b	-
Spirogyra sp.	-	-	c
Staurastrum sp.	-	b	-
Stigeoclonium sp.	-	-	c
Tetrastrum heteracanthum	-	b	-
Cyanophyta			
Anabaena circinalis	-	b	-
A. constricta	-	b	-
A. sphaerica	-	b	-
A. vaginicola	-	b	-
A. variabilis	-	b	-
Anabaenopsis arnoldii	-	b	-
Calothrix brevissima	-	-	c
C. javanica	-	-	c
Chroococcus minutus	a	b	-
C. turgidus	-	b	-
Cylindrospermum mucicola	-	b	c
Dactylococcopsis raphidioides	-	b	c
Lyngbya lucidum	-	b	-
Merismopedia punctata	-	b	-

contd./

Cyanophyta (contd.)	*Habitat*		
Microcystis aeruginosa	a	-	-
M. flos-aquae	a	-	-
Microchaete aeruginea	-	-	c
M. epiphytica	-	-	c
M. tenera	-	-	c
Monoraphidium contortum	-	b	-
Nodularia spumigena	-	b	c
Oscillatoria curviceps	-	b	c
O. schultzii	-	b	c
Phormidium angustissimum	-	b	-
P. autumnale	-	b	-
P. lutea	-	b	-
P. molle	-	b	-
P. mucicola	a	-	-
P. tenue			
Raphidiospsis curvata	-	b	-
Spirulina laxissima	-	b	-
S. platensis	-	b	-
S. subsala	-	b	-
Synechocystis aquatilis	a	b	-
Pyrrophyta			
Cymnodinium aeruginosum	-	b	-

* N.B. Several further forms of the genus *Nitzschia* were noted but no published descriptions were seen which were considered adequate to provide specific diagnosis.

TABLE 2.9

Gross productivity (mg O_2/hr) in the littoral region of the Southern Sector during June 1975

Sources	El Molo Island A 09.17 - 11.03	Shore, El Molo Bay B 12.25 - 14.32	West Shore South Island C 11.40 - 14.20	West Shore, 14.30 - 15.56
Attached algae:- $/m^2$ under flask	17.3	4.68	22.32	12.83
Attached algae:- $/m^2$ under funnel	-	-	16.85	7.34
Planktonic:- $/m^3$	367.3	-	213	-
$/m^2$ over 30 cm	110.2	-	63.9	-
Macrophyte:- $/m^2$	-	270.7	-	-
/g dry weight	-	6.93	-	-
Total, Benthic + Planktonic:- $/m^2$ over 30 cm	127.5	-	86.22 (flask) 80.75 (funnel)	-

TABLE 2.10

Ranges of gross production by algal and macrophyte associations in Lake Turkana estimated during the present study. Values are in mgC/m^2/day. Daily production of carbon in tonnes is also given for the four sectors of the main lake and for Ferguson's Gulf.

	Area (km^2)	Gross production (mgC/m^2/day)	Total gross daily production carbon (tonnes)
Open-water:-			
Northern Sector	2289	1315 - 6220	3008 - 14231
Central Sector	2925	194 - 3936	567 - 11512
Turkwell Sector	1027	1382	1419
Southern Sector	1319	259 - 293	341 - 386
Ferguson's Gulf	30	4147	124
Littoral Region:-			
Periphyton		25 - 77	
Plankton		221 - 381	
Periphyton + plankton		298 - 441	
Macrophytes:-			
El Molo Bay		931	
Allia Bay		4617	

CHAPTER 3

STUDIES ON THE ZOOPLANKTON OF LAKE TURKANA

by
A. J. D. Ferguson

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SUMMARY

ACKNOWLEDGEMENTS

REFERENCES

3. STUDIES ON THE ZOOPLANKTON OF LAKE TURKANA

A J D Ferguson

INTRODUCTION

WINBERG (1971) pointed out that detailed information on the breeding and growth of fish food organisms is a necessary part of accurate predictions of the potential production of fish. In order to establish the importance of the various invertebrate groups to the fishery in Lake Turkana a comprehensive study of their distribution, abundance, growth and predators was initiated in 1972. It was evident from an early stage in these studies that zooplankton was by far the most important category in the diet of many fish species. This section of the report described studies carried out on the zooplankton between December 1972 and May 1975.

METHODS

(a) COLLECTION OF ZOOPLANKTON SAMPLES

Quantitative zooplankton samples were collected with an opening and closing Clarke-Bumpus sampler with integral flow meter supplied by G & M Manufacturing Co Ltd. A full description of this apparatus and its use is given in EDMONDSON and WINBERG (1971). The Sampler was deployed from the 50 ft trawler R V HALCYON by hydraulic winch and hydrographic wire, a combination which ensured constant towing speeds during both vertical and horizontal tows. A 5 kg weight was used during horizontal tows and the relationship between warp length and sampling depth was investigated with Kelvin Tubes.

Preliminary trials in December 1972 showed that a sampling efficiency of 89% could be achieved with a No 20 net (aperture size 75µ) because phytoplankton densities were low. This meant that the whole zooplankton fauna, including nauplii and most eggs, could be sampled. This efficiency was however only attained with hauls of one minute or less during which time about 20 to 30 litres of water were sampled. When phytoplankton densities were found to be high, towing time was reduced to minute or less.

The number of samples taken at each site depended mainly on the depth. At least two vertical hauls were taken through the whole water column, thus reducing the error due to patchy distribution of the zooplankton. Horizontal tows were taken at the surface, 5 m, 10 m and thence downwards at 10 m intervals, the actual number of samples depending on the depth of the site. In very shallow water an oblique haul from the surface to the bottom and back was made instead of the vertical haul, and in rough weather the surface sample was occasionally omitted. Hydrographic observations described in Chapter 1, and metre tow net samples for young fish and prawns, were also taken at each site.

Sampling programme

The sampling routine was divided into three main phases:

(i) H1 site

Situated at a lake depth of about 80 m in the vicinity of Central Island (Fig. 1) this site was considered to be representative of open water conditions. It was planned that sampling should be carried out at site H1 at fortnightly intervals for a period of over a year, and this schedule was adhered to as closely as possible. Most of the work on vertical migration of the zooplankton over a series of 24 hr sampling sessions was carried out at this site.

(ii) 'Rectangular' cruises in the Central Sectors

It was planned that the two east-west transects (Fig. 3.1) should be carried out at monthly intervals on a rectangular cruise lasting two days.

(iii) Lakewide surveys

Lakewide surveys were carried out at approximately three month intervals and divided into two sections.

The North section included the 'Rectangular' cruise sites and the other sites shown in Figure 3.1. Subsidiary sites were also investigated as time and weather permitted. These cruises took about 5 days to complete but could be carried out in three days if only essential sites were visited.

The South section cruises started as soon after the North section as re-fuelling time and weather conditions permitted. This was normally about two days. The number of sites visited on southerly cruises depended very much on the wind conditions. Very strong winds were encountered in this part of the lake (see Chapter 1) which often made sampling impossible. As a result, these cruises took at least six days to complete.

Coverage of the whole lake therefore took between eight and thirteen days.

(b) PRESERVATION AND COUNTING

In most cases plankton samples were preserved with a modified Lugol's Iodine solution on site and taken to the laboratories for analysis. The standard Lugol's Iodine preservative was modified by adding a small amount of formalin solution. Sub-sampling was carried out by withdrawing aliquots from whole samples, placed in a polygonal box and stirred with a magnetic stirrer, with a wide mouthed syringe. The plankton in the sub-samples was identified and counted in 1 ml portions using a Sedgwick-Rafter counting chamber. The counts from each sample were continued until at least 100 of the most common zooplankters had been found.

Analysis of data collected from a series of replicate counts (20) of the same sample showed that, in most cases, the zooplankton was randomly distributed in the sub-smples (χ^2 values were between 95% confidence limits for agreement with Poisson series described by CROW and GARDNER (1959). The only categories found to have a contagious distribution in the sub-samples were copepod eggs and *Raphidiophrys pallida*. In both these cases contagious distributions were predictable because the eggs were found in discrete clutches and the latter had a tendency to clump in small groups.

Confidence limits for the sub-sample count as an estimate of the actual number in the sample, could be determined from the Tables of CROW and GARDNER (*op. cit.*) for the expectation of a Poisson variable using the total number of each category counted. The 95% confidence limits for the most common zooplankters (usually *Tropodiaptomus banforanus* were therefore less than -20% (+20.36% and -19.75% for 100 counted) but the confidence limits for less common species were usually wider. For example the 95% confidence limits for *Mesocyclops leuckarti* were about +30% and -24.66% and for the Cladocera, and Rotifers +50% and -36%. However, as time precluded extensive analysis of the patchy distribution of zooplankton in the lake, which would have required taking a large number of vertical hauls at each site, confidence limits of the samples as an estimate of the actual concentration have not been included. Sampling errors were considerably reduced by taking two vertical hauls at each site, but statistically significant spacial and temporal differences are only referred to in the text as being significant when they are greater than 100%, for most species.

RESULTS

SPECIES COMPOSITION

An inventory of zooplankton species is shown in Table 3.1 with common species asterixed. Most of the rare species were found near the shore or in the vicinity of the Omo River Delta.

The common Protozoan species *Raphidiophrys* cf *pallida* and *Vaginicola* sp. nov. were found all over the lake, but the less common species were restricted by their more specific habitat requirements. *Vaginicola subcylindrata* for example was only found attached to *Surirella* spp. diatoms and to *Microcysitis* spp. colonies. *Thuricola-folliculata* and *Sphaerotrichium elegans* were usually found nearer the shore. The former species was reported to be common in open water by WORTHINGTON and RICARDO (1936) but their drawings suggest that this was *Vaginicola* sp. nov. *Trichodina steni*, which is an ectoparasite of fish species, was also only found near the shore. Its restriction to inshore areas suggests that its hosts were littoral species such as *Sarotherodon niloticus* or *Haplochromis rudolfianus*.

Several species of epizoic and one species of epiphytic Peritrichs were also found in the plankton. The most interesting of these was a *Vorticella* species which used the loricae of *Vaginicola* sp. nov. as an attachment site. This relationship was first noticed by WORTHINGTON and RICARDO (1936) and will be discussed more extensively later (see page 171). Vorticellids were also found on *Microcystis* spp. colonies. Epizoic peritrichs similar to *Epistylis* spp. were found on the planktonic copepods, particularly *Mesocyclops leuckarti* and *Thermocyclops hyalinus*. Some adults of these species were heavily infested but the scarcity of the protozoan on copepodites stages suggests that their rapid moulting made them unsuitable attachment sites. The only protozoans found on all copepod stages wee single stalked Suctoria. These were commonly found on the nauplii of cyclopod copepods and *Tropodiaptomus banforanus*.

The only microturbellarian found in the zooplankton was *Gyratryx hermaphroditus*. This species is ubiquitous and has been recorded in several habitats in East Africa including Lake Victoria and Lake Naivasha (I am grateful to J O Young who supplied this information and identified the material). Eggs and juvenile stages of this species were also found in the samples.

During the present study eleven species of Rotifers were identified in zooplankton samples. The only genus not classified to species level was *Lecane* but specimens of this genus were rare and only found in association with *Microcystis* blooms in the open water.

The common open water Rotifers were *Brachionus plicatilis*, *Hexarthra jenkinae* and *Felinia terminalis*. *Felinia opalensis* and *Keratella tropica* were restricted to the open water of the Northern Sector and to the vicinity of the Omo Delta. *Brachionus dimidiatus*, *B. caudatus* and *B. calciflorus* occurred both in the open water of the Northern Sector and on the shore in all other lake sectors, but *B.quadridentatus* was only found in the littoral or in plankton samples taken near the shore. *Brachionus falcatus* which is usually found in shallow lakes in Europe and the tropics (RUTTNER-KOLISKO, 1974) was confined to marginal lagoons in the Lake Turkana area. A full discussion of the Rotifers found in relation to those found in other lakes is given later (page 182).

The only calanoid copepod found in the lake was *Tropodiaptomus banforanus*. This species was present in almost every sample. The cyclopoid copepods *Mesocyclops leuckarti* and *Thermocyclops hyalinus* were also very common, but the other cyclopoid copepods were rare and generally found near the shore.

Cladocera were less frequently encountered but not confined to any particular part of the lake. The most common species were *Diaphanosoma excisum* and *Moina brachiata*. *Hyalodaphnia barbata* and *Ceriodaphnia rigaudi* were found irregularly over the whole lake and had a rather patchy distribution. *Moina micrura* was only found in samples taken near the shore.

The majority of the common zooplankton species were found by WORTHINGTON and RICARDO (1936) in 1930-1931 with the notable exception of all but two of the Rotifer species. The apparent increase in the number of rotifer species probably results from the more intensive sampling of the present study. It is surprising, however, that *Felinia terminalis* and *Hexarthra jenkinae* were not found in 1930 by WORTHINGTON and RICARDO (*op. cit.*), since during the present studies the two species were relatively common in the area near Central Island where the earlier investigations were carried out.

RESULTS

THE DISTRIBUTION AND ABUNDANCE OF MAJOR ZOOPLANKTON SPECIES

(i) Vertical hauls

The following description of changes in areal density (numbers/m ^{2}) and concentration (numbers/l) of the major zooplankton species populations is based on the results of vertical hauls taken with the Clarke-Bumpus plankton sampler using a No 20 mesh net. The annual variations at the H1 site, just north of Central Island in 80 m of water, are described. These are followed by the results of vertical hauls from lakewide surveys with areal densities calculated from the depth of water at each site. The following surveys have been used to describe the 'seasonal' events.

(i)	March	1973	-Stable conditions
(ii)	June-July	1973	-Start of River Omo flood
(iii)	August	1974	-Flood season
(iv)	Sept-October	1973	-Flood season
(v)	December	1972 (South)]	Post-flood season
		1974 (North)]	

Results from 1974 have been used to supplement the available information from 1973. It was not assumed that the same cycle of changes in zooplankton population densities occurred each year.

In order to illustrate changes and differences in concentration and areal densities along the lake, the results from sites in the open water sectors (shown in Fig. 3.2) have been averaged and are illustrated graphically for each species below.

Protozoa

Raphidiophrys cf *pallida*

The results from H1 in 1973 (Fig. 3.3) show major peaks in abundance in June and mid August with subsidiary peaks in April and December. The concentration at this site varied from zero in January and July to over 15/l in June and August. For most of the year they accounted for between 2 and 12% of the total numbers of zooplankton, but during the peaks in June and August the proportion rose to over 40%. It is difficult to relate the fluctuations in this species population at H1 to any particular environmental changes but it is noticeable that the Rotifer populations are minimal in March-April and from June to August.

Lakewide distribution and areal densities of this species are shown in Figs. 3.4, 1-5. In March 1973 no *Raphidiophrys* cf *pallida* were found at sites in the Northern or Omo Sectors, and very few occurred in the northern half of the Central Sector. There was a noticeable increase in areal densities and concentration towards the south end of the lake and near the west coast of the Central Sectors. This southerly increase is also illustrated by Figure 3.5 where mean values for each Sector are shown. The mean concentration for the South Central Sectors and South Sectors are very similar, being 12.45 and

12.81/1 respectively, but mean densities increased from 312.0 x $10^3/m^2$ in the North Central Sector to 745.8 x $10^3/m^2$ in the Southern Sector, thus higher area densities in the south were a result of greater lake depths.

By June-July 1973 (Fig. 3.4.1) there was an overall increase in the areal densities and concentration of this species. Significant concentrations were now found in the Northern Sector but the protozoan was still absent from samples taken near the Omo Delta. Figure 3.5 shows that the mean concentration and densities in the two Central Sectors had increased considerably and that the concentration in the Southern Sector had decreased from 12.45/1 in March to 7.67/1 in June-July. It is also interesting to note that the west to east increase in areal densities seen in the Central Sectors in March was not evident in June-July but was found in the Turkwell Sector with relatively low densities near the Kerio River mouth.

During August (1974) the number of sampling sites was relatively low but a general distribution pattern is still evident. Very few Raphidiophrys were found south of the North Central Sector but low concentrations of 2.17/1 were present near the Omo Delta, with very low concentrations in the Southern Sector.

In September-October 1973 (Fig. 3.4.4) the density distribution pattern was rather similar to that seen in August 1974 with relatively low numbers found at most of the sites. The concentrations in the Turkwell and Southern Sectors (0.48 and 1.86/1 respectively) were lower than the mean concentration for the Central Sector (5.5/1).

In December (1972/4) the pattern of density distribution (Fig. 3.4.5) was again similar with low, evenly distributed values. However, as in the pre-flood period, the species was again absent from the vicinity of the Omo Delta. Mean concentrations ranged from 1.05/1 to 7.66/1.

It is evident from these results that the annual cycle of changes shown in Figure 3.3 for the H1 site is an expression of a more complex cycle of events which takes place over the whole lake. This can be best described as a northward shift in the region of peak abundance from the Southern Sector in March to the Central Sector in June and to the Omo Delta in August. The peak then apparently moves south in December when the species had disappeared from the Omo Delta region. Apart from this longitudinal movement there is also an annual change in overall abundance with maximum concentrations in June and minimum concentrations in December.

Vaginicola sp. nov.

The results from H1 (Fig. 3.6) show that this species had a fairly straightforward annual cycle. A minor peak in abundance of 9.09/1 was observed in February followed by a large increase to 50.9/1 in early March. For the remainder of the year the species occurred irregularly in small numbers. In March this species accounted for 45.65% of the total numbers of zooplankton compared with less than 1.5% later in the year.

Lakewide surveys indicate that a similar pattern of events occurred over the whole lake. During March 1973 (Fig. 3.7.1) areal densities of over 1000 x $10^3/m^2$ were found at nearly all the sites away from the shore. Relatively low densities were noted at inshore sites. Calculations of mean areal densities (Fig. 3.8) indicate maximum values in the South Central Sector, but the actual concentrations decreased significantly towards the Southern Sector.

By June-July, Vaginicola sp. nov. had disappeared from many of the sites or was only found in very low numbers. No particular distribution pattern is discernable and the species extended irregularly throughout all lake Sectors.

During August 1974 the number of samples was small and the results indicate a patchy distribution with relatively large densities near Central Island and Moite but none in samples taken north of North Island.

In September-October 1973 densities in the Turkwell and Southern Sectors were greater than those found in June-July, giving rise to a pattern of increasing densities towards the south end of the lake. This trend was also indicated by the results for December shown in Figure 3.8.

The overall pattern of change in density distributions was therefore very different from that of the other common protozoan Raphidiophrys cf pallida, particularly in the early part of the year. Generally, distributions of the two are related but successional.

Vorticellids associated with Vaginicola

These sessile protozoa live in a truly planktonic environment by attachment to the loricae of Vaginicola sp. nov. and to blue-green algal colonies. Their association with Vaginicola sp. nov. was first observed in Lake Turkana by WORTHINGTON and RICARDO (1936), who described the depth distribution of these organisms in relation to Vaginicola sp. nov. and their loricae. They found that the Vorticellids were able to invade the loricae even when occupied by the rightful owner, and that the number of empty loricae invaded by Vorticellids exceeded those occupied by Vaginicola sp. nov. The results from the present survey showed that a similar pattern was found at H1 throughout the year, except that the number of loricae with Vorticellids only exceeded the number of Vaginicola sp. nov. on 20th February and 6th April 1973. On both these occasions the Vaginicola sp. nov. were declining. The results also showed that the Vorticellids only invaded the loricae containing Vaginicola in any numbers between March and June. A similar situation was found over the rest of the lake.

In view of the fact that the Vorticellids only invade the loricae containing Vaginicola at certain times of the year it seems that the relationship is unlikely to be mutually beneficial and rarely detrimental to the Vaginicola sp. nov. populations. The relationship would therefore be described as commensal rather than parasitic or symbiotic.

Rotifera

Hexarthra jenkinae

During the present survey this species was by far the most common rotifer at the H1 site. The results in Figure 3.9 show that there were three main peaks in abundance. During the first peak in February a maximum concentrtion of 1.1/1 was reached. After a second peak of 0.98/1 in April numbers declined, and none was observed in June or July. From August onwards the species gradually increased to reach a third but smaller peak of 0.67/1 in December.

The results from lakewide surveys showed a relatively clear pattern of density distributions despite the rather low numbers. In March, when the density at site H1 was low, there was an obvious decrease in densities from the Omo Delta towards the south end of the lake. This was most evident from the mean concentrations shown in Figure 3.11. The concentration near the Omo Delta of 14.8/1 was the highest recorded during this survey. Depsite the rapid decline in densities south of the Northern Sector, the species extended in small numbers down to the south end of the lake.

By June-July (Fig. 3.10.2) the north-south density gradient was less evident as there had been a significant reduction in numbers near the Omo Delta. In August (1974) densities at the north end of the lake were higher, but as with the previous surveys, small numbers were found at most of the other sites throughout the lake. During cruises in September no samples were taken in the Northern or Omo Sectors but results indicate that low densities over the Central, Turkwell and Southern Sectors persisted during the flood season.

Results from December (Fig. 3.10.5) show a more patchy distribution but indicate an increase in the Hexarthra jenkinae populations in the North and Omo Sectors. Relatively high numbers were also found in the Central Sector but further south they were only found at one of the six sampling sites.

The annual cycle for Hexarthra jenkinae was therefore relatively straightforward. Small concentrations persisted throughout the year over the Central, Turkwell and Southern Sectors. The annual fluctuations observed at the H1 site probably describe the fluctuations in this area most accurately. Density changes in the Omo and Northern Sectors were greater and somewhat different, with a significant decline in the population at the onset of the flood season in June-July. The gradient of decreasing concentrations and densities from the north end of the lake towards the Southern Sector persisted throughout the year (see Fig. 3.11).

Brachionus plicatilis

The results from H1 show that this species was only found between December and March and accounted for 0.4 to 3.6% of the total numbers of zooplankters. A maximum concentration of 0.99/1 was found at this site in late February.

This situation is also explained more readily by comparison with the data from lakewide cruises. Results (Fig. 3.14) show that Brachionus plicatilis was largely confined to the north end of the lake. Maximum concentrations of 35.1/1 were found near the Omo Delta in March at which time they were also common in the Northern and North Central Sectors (Fig. 3.15). Very few occurred further south.

The present species of B. plicatilis in the open water was commonly encountered at shore survey sites throughout the lake, thus indicating that this species was only truly planktonic in the Northern Sector in Lake Turkana. The fact that small numbers were found in the open water of the Central, Turkwell and South Sectors suggests that the rotifer tended to be carried from the shore by wind generated currents. This is supported by meteorological evidence (see Chapter 1) which shows that the highest winds occur in the southern basin of the lake.

Crustacea

Tropodiaptomus banforanus

This species was normally the most abundant zooplankter and accounted for a mean of 28.8% by numbers of the total population, with the proportion varying from 13.8% in March to 48.0% in January. Figure 3.16 shows the relatively small but significant changes in the areal density of this species observed at H1 site in 1973. The overall mean concentration at this site was 7.31/1 (584.47 x $10^3/m^2$) with a range from a minimum of 3.3/1 in December to 15.39/1 in March. The largest fluctuations in the numbers of this species occurred in the early part of the year with a sharp rise from 4.1/1 in mid-February to the annual maximum in March. After this peak, concentrations tended to decrease slowly in subsequent months, but during August a sudden increase in concentration to 9.46/1 briefly interrupted the decline. The concentrations had fallen to 6.1/1 by the end of August and reached a minimum of 3.3/1 in December.

It is interesting to note that despite only six visits to this site during 1974, the mean concentration of 7.73/1 was only 0.4/1 higher than the mean of 7.31/1 found in 1973.

The areal densities found from vertical hauls on lakewide surveys at different times of the year are shown in Figures 3.17, 1-5.

Results from March 1973 show that areal densities at most sites were greater than 1000 x $10^3/m^2$. However, densities near the west coast of the Central Sectors, and at the site near the Omo Delta, were significantly lower (less than 300 x $10^3/m^2$). Unusually high densities were recorded in the open water of the Southern Sector and near the east coast of the North Central Sector. In the latter case the density was greater than 3000 x $10^3/m^2$. The average densities for each sector shown in Figure 3.18 indicate that the distribution of T. banforanus was relatively uniform, but the concentrations in the Northern Sector were significantly higher. The two Northern Sector sites concentrations were greater than 50/1 compared with between 20-26/1 in the open water of the other sectors. It is interesting to note that, although the areal density near the Omo Delta was only 144 x $10^3/m^2$ compared with over 1000 x $10^3/m^2$ in the other sector, the actual concentration of 20.6/1 was similar to those recorded in other sectors.

In June-July there was a significant decrease in the Tropodiaptomus banforanus population in the Omo and Northern Sectors coinciding with the influx of fresh, brown water from the River Omo. Densities of over 1000 x $10^3/m^2$ in the southern part of the Northern Sector were still comparable with those of the March survey.

Further south, densities and concentrations were also similar to those found in the March survey, but significant reductions were evident at some sites. For example the areal density at the Koobi Fora site on the east coast of the North Central Sector fell from 3267 x $10^3/m^2$ in March to 486.4 x $10^3/m^2$ in June-July. The Turkwell Sector was not sampled in the March survey, but the June-July results indicate that densities in this Sector were similar to those found in other parts of the lake. Maximum densities in the Turkwell Sector were found near the east coast, but samples from the sites near to and south of Merriar Spit indicated significantly lower densities near the west coast. This apparent gradient of increasing densities from west to east was noted in the Central Sectors during the March survey. The concentrations and areal densities in the Southern Sector were slightly lower than those found in March, with a drop in mean density from 1534.0 x $10^3/m^2$ to 1236 x $10^3/m^2$.

During August 1974 the number of sites visited was smaller but results indicate lower densities in more northerly areas including the site in the southern part of the Northern Sector. The areal density at this site was only 270.8 x $10^3/m^2$ (10.5/1) compared with 830.6 x $10^3/m^2$ (28.3/1) in the June-July 1973 survey. The results from sites in the Central Sectors also indicate lower densities than during June-July 1973, but those from the Southern Sector were similar.

In September-October 1973 the situation had changed considerably, with a reduction in *T. banforanus* population in the southern basin and an overall increase in the densities and concentrations in the Central Sector, thus reversing the trend seen in August 1974.

Results from December 1972/4 show that the trend apparently persisted, with a further reduction in both concentrations and densities in the Southern Sector from 744.8 x $10^3/m^2$ in September-October to 372.4 x $10^3/m^2$. In contrast, densities in the north of the lake had increased. The concentration near the Omo Delta was now maximal at 44.6/1, and the mean concentration in the Northern Sector had returned to pre-flood levels of above 50/1.

These results suggest that two main waves of events in the *Tropodiaptomus banforanus* populations occurred each year. It appears that an increase in the population occurred in the north end of the lake after the flood season in December, while population levels further down the lake were minimal. This was followed by a wave of increasing population levels moving south and passing through the Central Sector in March (including H1) and reaching the Southern Sector in August. The relatively high densities in the Northern Sector were probably maintained until the start of the Omo flood season in June-July when much reduced population densities were found in samples collected in the brown, turbid water near the delta. This wave of reduction in the populations moved rapidly down the lake, reaching the Turkwell Sector in August and the Southern Sector in September. It is interesting to note that the chain of events parallels the spreading influence of the inflowing fresh water shown by the conductivity measurements in Chapter 1 although with the exception of the most northerly areas, the two sequences are probably not directly connected. This description somewhat oversimplifies the situation, because other changes occur in the *T. banforanus* populations which are not related to these events. This is particularly true of the large differences in the populations on the east and west sides of the lake in March. Reduction of zooplankton populations on the west coast was probably caused by predation effects of the larger fish stocks in this area of the lake (see Chapter 8).

Mesocyclops leuckarti

As the nauplii of this species were not readily distinguishable from those of the other cyclopod copepods, the following description is based on the copepodite and adult stages only.

The results from the H1 site indicate that *Mesocyclops leuckarti* was normally the second most abundant species, forming an overall mean of 10.1% by numbers of the total zooplankters, with an average concentration of 4.72/l in 1973 and 3.94/l in 1974. Figure 3.19 illustrates the changes in areal density observed at this site in 1973. A minimum concentration of 1.25/l was recorded in late January, after which the populations increased gradually in February to reach 5.9/l in March. Subsequently the concentrations fluctuated between 4.4 to 5.8/l until the end of August. By mid-October they had fallen to a level of 2.2/l before increasing rapidly in November to reach an annual peak of 8.25/l in December. At the time of this peak they dominated catches at site H1, forming 34.2% by numbers of all zooplankters.

The areal densities observed on lakewide cruises are shown in Figures 3.20, 1-5. The results from March 1973 show several interesting features including a gradual decrease in densities from the Omo Delta area southwards (Fig. 3.20.1). At this time, *Mesocyclops leuckarti* was by far the most abundant species near the Omo Delta with concentrations of 81.6/l compared with only 31.2/l in the case of *Tropodiaptomus banforanus*. Areal densities further south were variable but noticeably low at sites near the west coast of the Central Sectors, and in the area just south of Central Island. The apparent gradient of increasing densities from west to east in the North Central Sector was also seen for several other species. In the Southern Sector the population levels were rather variable, with low densities near the east coast. The mean concentration of 5.56/l (271.9 x $10^3/m^2$) significantly lower than the 14.5/l (384.6 x 10^3 $/m^2$) found in the Northern Sector.

Results from June-July show quite a different pattern of density distribution (Fig. 3.20.2). The concentration near the Omo Delta dropped from 81.6/l in March to 7.1/l and (in the Northern Sector) from 86.6/l to 14.5/l. In contrast there was an increase in areal densities and concentration at most sites further south. The changes in the Southern Central Sector were most dramatic, with an increase in mean concentration from 4.4/l in March to 34.8/l in June-July. Although the Turkwell Sector was not sampled in March, it may be deduced from the trend of increasing population levels from north to south shown in Figure 3.21 that population levels in this sector also increased. The mean concentrations in the southern basin increased from 5.6/l to 8.0/l.

The pattern of density distribution of *Mesocyclops leuckarti* seen in August 1974 was similar to that found in March 1973, but concentrations and density levels were generally lower except in the southern basin. A concentration of 60.6/l recorded at the site near the Omo Delta was also higher than in March. If it is considered that a similar cycle of change took place each year, then the biggest decrease occurred in the South Central Sector where mean concentration dropped from 34.8/1 in June 1973 to 5.74/1 in August 1974. Evidence for the repeatability of this particular trend is seen from the results of the September-October 1973 surveys (Fig. 3.20.4) which show that densities in the Central and Southern Sectors of the lake were significantly lower than those found in June-July 1973. The tendency for concentrations to decrease towards the south end of the lake is illustrated by the fall in mean concentration from 11.4/1 in the North Central Sector to 4.68/1 in the Southern Sector.

Results from the December 1972/4 surveys indicate a situation similar to that observed in September-October 1973, and in some respects comparable with the results from March 1973. The concentrations in the Northern Sector were relatively high at 27.0/1 and declined further south to means of 4.8/1 in the Turkwell Sector and 6.6/1 in the Southern Sector. In the Central Sectors there was a marked east to west density gradient with very low population levels near the west coast paralleling the situation found in March 1973.

The pattern of change in density at site H1 is not easily relted to the situation found over the rest of the lake, apparently because the site is positioned at the fulcrum of the longitudinal oscillations. In March, densities and concentrations were higher to the north of H1 and lower to the south, but in June-July the situation was reversed. In September-October, densities were similar over most of the lake and in December density distribution had generally reverted to the pattern seen in March.

Thermocyclops hyalinus

As the nauplii of this species were not easily distinguishable from those of other cyclopoid copepods, the following description is based on the areal densities and concentrations of copepodite and adult stages only.

At site H1 Thermocyclops hyalinus had a mean concentration of 1.56/1 (125.2 x 10^3 /m^2) in 1973 (1.69/1 in 1974) and formed an average of 5.35% by number of the total zooplankters. Figure 3.22 shows the changes in areal density and concentration observed at this site in 1973. These results indicate that the size of the population fluctuated more than the other copepods and that there were two major peaks in abundance. Minimum concentration of 0.2/1 was observed in February after which the concentrations increased to a peak of 2.9/1 in March. The concentration decreased in April and remained relatively steady at between 0.8-1.1/1 until the end of July. A second but larger peak of 3.6/1 was observed in August followed by a return to lower densities. BURGIS (1971) also found peaks in the abundance of this species in March and August in Lake George (Uganda), but the concentrations were very much higher (up to 600/1).

The areal density distribution maps from lakewide surveys shown in Figures 3.23, 1-5 show considerable fluctuations in the population of T. hyalinus elsewhere in the lake. In March 1973 the highest densities were found near the east coast of the Central Sectors and in the Northern Sector. As the concentrations near the west coast were relatively low there was a noticeable east-west density gradient. Results from the Southern Sector were more varied with concentrations ranging from 0.7/1 near Porr Point to 10.1/1 at the most southerly site. Mean concentrations from different sectors illustrated in

Figure 3.24 indicate a southward decrease along the axis of the lake, but local variations in the population of this species were greater than those of most of the other zooplankton at this time.

The results for June-July 1973 show that a radical change in the density distributions had taken place. Concentrations in the Northern Sector and the Omo Delta region had been reduced to a minimum, and at the site near Koobi Fora in the North Central Sector concentrations had declined from 23.6/l in March to 1.3/l. Densities in the Turkwell Sector were relatively high, particuarly south of Meriar, and populations in the Southern Sector had increased from 3.5/l (178.3 x 10^3 /m^2) to 10.04/l (638.9 x 10^3/m^2), contrasting strongly with the decline in the north. This resulted in a complete reversal of the density and concentration quotients along the lake. It was also noticeable that densities at sites near the west coast were no longer significantly lower than those near the east coast.

During August 1974 the Thermocyclops hyalinus populations over the whole lake were even lower, particularly in the North and Central Sectors. The only site where significant numbers were observed was in the Southern Sector west of South Island. However, even at this site the concentration was only 2.2/l compared with 7.6/l at the same site in June-July 1973.

By September-October 1973, areal densities were generally higher than those observed in August 1974, with the possible exception of the South Island region. The mean areal density in the North Central Sector was higher than in June 1973 or August 1974 with an average concentration of 5.2/l. Figure 3.24 indicates that the mean areal densities were similar in each sector but the concentrations declined towards the Southern Sector.

In December 1972/4 densities in the Northern Sector and in the Turkwell Sector were low, but there was a noticeable increase in the areal densities from north to south at sites in the open water.

The fluctuations in the Thermocyclops hyalinus population at H1 with two peaks in abundance during the year reflect the situation found over the rest of the lake, but they do not reflect the marked longitudinal differences seen in the lakewide surveys.

Cyclopoid copepod nauplii

The nauplii of the two major zooplankton cyclopoid copepods Mesocyclops leuckarti and Thermocyclops hyalinus were not easily distinguished and have therefore been considered jointly.

At H1 the concentration varied from 1.0/l in early January to 5.1/l in June and formed an average of 10.55% by number of total zooplankters. Changes in areal density and concentration observed at this site are shown in Figure 3.25 which illustrates a gradual but uneven increase in concentration which continued from early January to reach a peak in June. Numbers declined during July and August but subsequently rose to reach a further peak in November. The fluctuations are certainly related to changes in concentration of adults of both species concerned but are not as marked as those of temperate populations. Consequently it has not been possible to correlate the changes with those of later stages. It seems likely, however, that nauplii present during the period from April to June were mainly those of Mesocyclops leuckarti since Thermocyclops hyalinus densities were minimal at this time.

The results from lakewide surveys are also difficult to interpret because of the two species involved, but several trends were evident. In March the maximum concentrations of 315/l found near the mouth of the River Omo were related to the relatively high concentrations of the later stages of both cyclopoid species at the site (Figs. 3.20.1 and 3.23.1). Areal densities and concentrations in the Central Sectors were generally very similar at all sites and as noted previously, marked east-west density gradients were noted in the later stages of both species. The high concentrations of nauplii in the Southern Sector also contrasted with the pattern observed in the later stages. The areal density of the nauplii reached 4390 x $10^3/m^2$ at the site west of South Island.

During the June-July survey, results from the north end of the lake indicate a reduction in the concentrations to only 5.9/l (36 x $10^3/m^2$) which is correlated with a similar reduction in the concentrations of later stages. Maximum naupliar densities were found in the South Central Sector, and relatively low densities were found in the Turkwell and Southern Sectors. This contrasts strongly with the distributions of both species of adults and copepodites (Figs. 3.20.2 and 3.23.2).

Results for August 1974 indicate that the density distribution was very similar to that of Mesocyclops leuckarti. Since none of the later stages of Thermocyclops hyalinus were found north of North Island, it may be assumed that the nauplii were mainly of Mesocyclops leuckarti.

In September-October the distribution pattern of nauplii was similar to that of the later stages of both M. leuckarti and T. hyalinus with a marked tendency for higher densities at the south end of the lake. This situation differs markedly from that observed in March and June when distributions of the three categories were different.

During December 1972/74 the density distribution of the nauplii was rather patchy (Fig. 3.26.5) and in this respect was similar to that found for the later stages of both M. leuckarti and T. hyalinus. As the former species dominated the northern part of the lake at this time with a mean concentration of 27/l compared with 3.2/l of T. hyalinus, it seems likely that most of the nauplii in this area were those of Mesocyclops leuckarti.

Cladocera

Diaphanosoma excisum

Although D. excisum was the most common Cladoceran species in the lake, the species formed an average of only 3.3% by number of the total zooplankters at the H1 site. An average concentration of 0.8/l was recorded ranging from zero in November to 3.3/l in January. The changes in areal density and concentration at the H1 site in 1973 are illustrated in Figure 3.27 which shows a markedly different pattern from those observed in copepods. Concentrations in the early part of the year were variable with three peaks in abundance. After the third peak in May and June, the population declined and densities remained below 0.25/l from July to November.

The results from lakewide surveys shown in Figures 3.28, 1-5 indicate that a similar pattern of events occurs over most of the lake in populations of this species. In March 1973 densities were variable, but mean concentrations for each Sector (Fig. 3.28.1) indicate that populations at the south end were significantly smaller than those in the north. It is interesting to note that none was found at the site near the west coast of the Central Sectors.

- In June-July 1974, densities in the Northern Sector were variable but higher than the Omo Delta area and the North Central Sector. South of Central Island they were more evenly distributed but increased in number towards the Southern Sector. It is significant that the decrease in density in the Omo Sector at the start of the flood season noted in D. excisum, also occurred in many other zooplankton species. Further south the density of $383.4 \times 10^3/m^2$ near the west coast of the Northern Sector was the highest recorded for this species.

During August 1974, much lower densities of Diaphanosoma excisum were noted in the Northern Sector but populations increased gradually towards the south end of the lake. This situation suggests a further reduction in the population, coinciding with the spread of the Omo River input.

The results from surveys in September and October 1973 indicate a continuation of this trend with lower areal densities in the South Central and Turkwell Sectors. In the Southern Sector densities were also lower but the mean values (Fig. 3.29) indicate a distinct trend of increasing population levels towards the south end of the lake.

The pattern of density distribution in December 1972/4 shows that the population was greater than that found in September-October 1973, and indicates a recovery following the flood season, particularly in the Northern Sector. The situation was similar to that found in March 1973.

It is evident that the decline in the population seen at H1 in July reflects a general decline in the numbers of D. excisum during the flood season, which starts at the Omo Delta in June and continues southward to reach the Turkwell and Southern Sectors in October. The concentrations in the latter Sector are least affected and are maintained at an average above 7.0/l all year. It also appears that there was a general recovery of the population in December.

Moina brachiata

This species was only found at irregular intervals at site H1 and reached a maximum concentrtion of 1.1/l in mid-January. During 1973 M. brachiata formed a mean of 0.56% by number of the total zooplankters most of which were recorded in samples between December and mid-June. Thus the annual cycle for this species at H1 resembles that of Diaphanosoma excisum.

Trends in the lakewide distribution of M. brachiata (Figs. 3.30-31) are difficult to interpret due to low densities and patchy distribution. In March 1973 areal densities in the open water in the north were higher than elsewhere but concentrations near the shore were generally very low. The results indicate, however, that the species had a lakewide distribution, although very few occurred in the South

Central or Southern Sectors. In June-July 1973 small numbers were noted in all sectors, reaching a maximum of less than 100 x $10^3/m^2$ in the western half of the Northern Sector.

During August 1974 the species was only found at three of the ten sites investigated, and these were widely scattered through the lake. The somewhat patchy nature of distribution is illustrated by the high density of 141.9 x $10^3/m^2$ found at the site west of South Island.

The distribution pattern found in September-October 1973 resembled the situation noted in August 1974 with the species occurring at five of the fifteen sites. During December none was found south of Central Island.

Ceriodaphnia rigaudi

Mean concentrations of 0.08/1 and 0.04/1 were noted for C. rigaudi at site H1 during 1973 and 1974 respectively. The species formed a 0.3% by number of the total zooplankters. They were found at irregular intervals from October to May, reaching a maximum concentration of 0.4/1 in February. In common with other Cladocera, low concentrations were found between March and November and the species was absent from samples between July and the end of August.

The results of lakewide surveys in Figures 3.32, 1-5 indicate that, like Moina brachiata, the distribution was irregular and patchy but not localised. In March 1973 the maximum density of 31.2 x $10^3/m^2$ was found near Central Island and the species was generally scarce or absent from many of the other sites. A similar situation was observed during the June-July 1973 survey (Fig. 3.32.2) when the species was absent from half the sites visited. During this cruise a maximum density of 337.05 x $10^3/m^2$ was recorded at the site just north of North Island.

In August 1974, Ceriodaphnia rigaudi was only found at one site and the species was also scarce during September-October 1974. Concentrations were generally higher during December but the distribution was again patchy.

Despite the inconsistent results from Moina brachiata the species resembled other Cladocerans in that it was adversely affected by the inflowing turbid water from the Omo River during the flood season, with a general period of recovery during the post-flood season.

DISCUSSION

Protozoa

HUTCHINSON (1967) and WETZEL (1975) in their discussions of zooplankton studies, conclude that protozoans are normally insignificant in terms of their numbers and biomass in lakes. However, WATSON (1974) in his review of studies on the Great Lakes of Canada comments that relatively few observations have been made on protozoa in recent years and thus their importance may have been underestimated.

In Lake Turkana, and possibly in other tropical lakes, this group may form an important link in the food cycles. WORTHINGTON and RICARDO (1936) found significant numbers of Heliozoans in Lakes Turkana, Naivasha and Edward and results from the present survey show that, in Lake Turkana, they may form up to 75% of the total numbers of zooplankters with concentrations of up to 80/l. It is interesting to note that similar concentrations of protozoa have been found in summer zooplankton populations in the Great Lakes of Canada. DAVIS (1969) working on Lake Erie, and LEACH (1973) working on Lake St Clair, found concentrations of protozoans were around 40/l, but in these cases they never formed more than 40% of the total number of zooplankters and averaged only 8%.

The potentially high reproductive rate of the protozoa compared with other zooplankters is an important factor to be considered. As the total generation time may be only a matter of hours (e.g. KITCHING, 1957) they may achieve a high Production/Biomass (P/B) ratio. This was emphasised by the work of SOROKIN and PAVELJIVA (1972) on Lake Dalnec in Russia. In this case protozoans contributed 66.9% of the total zooplankton production with a P/B ratio of 6.7. The relatively high production rate of the protozoa in Lake Dalnec may be exceptional, but the capacity for rapid increase of Lake Turkana protozoa is illustrated by the 200-fold increase in the *Vaginicola* sp. nov. population at site H1 between 20th February and 8th March 1973 (16 days). Heavy predation by larger zooplankters would tend to keep protozoan biomass and numbers minimal, thus obscuring the group's importance. Unfortunately, facilities for studying the growth rates of the protozoa were not available, but it is noticeable from the results that the *Raphidiophrys* cf *pallida* population increased when Cladocera and Rotifer populations were low.

The factors affecting the abundance of the protozoa in Lake Turkana remain obscure. The relatively high salinity is unlikely to be a limiting factor because many species are unusually tolerant of salinity changes. For example, FINLEY (1930) was able to culture 21 freshwater protozoan species in undiluted sea water.

Unfortunately the exact nutritional requirements of phagotrophic protozoans are known only for a few species (NOLAND and GOJDICS, 1967) but it is likely that bacteria are the main food source of the protozoans in Lake Turkana. As we have no knowledge of the distribution or abundance of bacteria in the lake, it is difficult to evaluate the importance of these organisms as a factor limiting the abundance of the Protozoa. NOLAND (1925) and SANDON (1932) regard food as the most important limiting factor to the distribution and abundance of free living protozoa. It is evident, however, from the observed differences in the population dynamics of the two main protozoan zooplankters *Raphidiophrys* cf *pallida* and *Vaginicola* sp. nov., that the factors governing the abundance of these species is in some way different. Peak densities of *Raphidiophrys* cf *pallida* moved up the lake in a wave form starting in the Southern Sector in March and reaching the Omo Delta area in August. In contrast *Vaginicola* sp. nov. was found in maximum numbers all over the lake in March. This gives rise to a successional appearance in the concentration of the two species at the H1 site (see Figs. 3.3 and 3.6) with maximum concentrations of *Vaginicola* sp. nov. in March followed by high concentrations of *Raphidiophrys* cf *pallida* in June and August. This succession was also found in the Northern and North Central Sectors but not in the Southern Sector. Despite these differences, the contribution of the Protozoa in different parts of the lake remained remarkably similar. Figure 3.34 shows that the group increased in proportion at sites down the mid-line of the lake from the Omo Delta region to the South Central Sector and then declined in importance towards the south end of the lake in March, June and August. This longitudinal change is related to differences in the abundance of the other major groups. At the north end, Rotifers and *Mesocyclops leuckarti* were found in higher proportions, and *Tropodiaptomus banforanus* increased in importance towards the south end. The lack of any specific information on the factors limiting the size of the protozoan populations precludes any conclusion on the reasons for this rather obvious spacial difference in their relative abundance. However, the reduction in the protozoan populations in the north end may indicate competition for food with the microphagous rotifer species which increase in importance in this area.

Rotifera

The results for all three common open water rotifers clearly show that maximum concentrations and areal densities were found at the north end of the lake, and that they were correspondingly rare in the south. The species diversity was also greater in the north, and several species including *Keratella tropica* and *Felinia opalensis* were found in this area. This situation is further emphasised by the percentage contribution of the rotifers to the total number of zooplankters shown in Figure 3.35 which indicates that the proportion of rotifers decreases very rapidly with increasing distance from the River Omo Delta. A similar situation was found by GREEN (1967a) near the Semliki River and Victoria Nile inflows to Lake Albert, and by BURGIS (personal communication) near the inflows to Lake George. GREEN (*op. cit.*) attributes the increase in diversity and proportion of rotifers near the inflows to the rate of water movement being sufficient for the development of a more typically riverine type of zooplankton. He found that samples taken near the inflow to Lake Albert were very similar to those collected from the River Sokoto in Nigeria (GREEN, 1960) with *Keratella tropica* and *Brachionus caudatus* dominant. The situation in Lake Turkana is also similar in that *Keratella tropica* was only found near the Omo River and that *B. caudatus* was often dominant in this region.

No single environmental factor governs the distribution and abundance of the rotifers in Lake Turkana but the relatively low concentrations, numbers of species and proportions may be partly explained by the effects of the relatively high salinity. Figure 3.36 illustrates the distribution of species found in Lake Turkana and in other African lakes, and indicates the total number of species found by various authors. This clearly shows that many of these species are not found in lakes with conductivities greater than 3500 µS/cm. k25 °C and that *Hexarthra jenkinae* and *Brachionus dimidiatus* have not been found in lakes with conductivities less than Lake Turkana. The presence of *Brachionus plicatilis* in Lake Edward (DE BEAUCHAMP, 1932) which has a conductivity of around 800-1100 µS/cm k20°C (TALLING and TALLING, 1965) and in the Kataboi Gorge Pools (conductivity 800 µS/cm k25° C) during the present survey indicates that the distribution of this species is intermediate. The relationship between rotifer species distributions and the water chemistry of relatively saline lakes has been discussed on a world wide basis by RUTTNER-KOLISKO (1971), who has shown that the species composition can be used to indicate the type of salinity. For example, the combination of *Brachionus plicatilis* with *Hexarthra jenkinae*, found in Lake Turkana, indicates that the water has a high soda content. This is borne out by the results of chemical analyses given in Chapter 1. It also appears from the East African lakes (Fig. 3.36) that the presence of

Brachionus dimidiatus indicates that the water has a high soda component. The reasons for the differing tolerances of rotifer species to high salinities is not clear but EPP and WINSTON (1977) have recently shown that *Brachionus plicatilis* can alter the osmolarity of its body fluids directly with that of the external conditions up to 957 m-osmal/l. However, they also showed that this species was unable to adapt to concentrations of less than 32 m-osmal/l and are thus confined to alkaline or brackish waters. They concluded that its absence from acid water was due to low salt concentrations associated with these conditions rather than low pH. This experimental evidence is supported by the field observations shown in Figure 3.36 which indicates that *Brachionus plicatilis* has not been found in East African lakes with conductivities less than 800 μS/cm k25°C.

Further evidence to support the hypothesis that some species are excluded from Lake Turkana by salinity comes from the survey of rotifer populations in Lake Chad by ROBINSON and ROBINSON (1971). This study showed that in most areas where the conductivity was around 600 μS/cm k25°C, *Keratella tropica* contributed more than 50% of the total rotifer population, but in the north region where the conductivity was normally above 1100 μS/cm k25° C the *Keratella tropica* population was much reduced and *Brachionus caudatus* was dominant. This was the only area where they found *Brachionus plicatilis*. It is interesting to note that the only rotifers found by PURRIOT *et al* (1967) in the alkaline pools near Lake Chad, which had even higher conductivities, were *B. dimidiatus* and *B. plicatilis*.

The low number of species and low densities of rotifers in Lake Turkana may also be partly explained by the Size Efficiency Hypothesis proposed by BROOKS and DODSON (1965). This was proposed in order to explain the commonly observed inverse relationship between the numbers of small and large bodied zooplankters found in freshwater lakes. The removal of large bodied zooplankters by predatory fish often results in higher concentrations of smaller, less efficient filter feeding zooplankters. It would be concluded therefore that the dominance of copepods in the open water of Lake Turkana was due to low predation pressure and the competitive exclusion of the Rotifera. However, as HALL *et al* (1976) in their review of this topic have pointed out, many other factors such as resource partitioning by differences in vertical distribution or diel feeding patterns and the effects of predation pressure would have to be fully investigated before one could be certain that this was the case in Lake Turkana. GREEN (1967a) uses this hypothesis to explain the dearth of planktonic rotifers in the middle of Lake Albert.

Although the population dynamics and seasonal successions in rotifer populations in temperate lakes are well known (RUTTNER-KOLISKO, 1974) there are few detailed accounts of the seasonal changes in the abundance of rotifers in equatorial African lakes. GREEN (1967a) has studied changes in the abundance of rotifers from samples taken at monthly intervals over one year in Lake Albert. Unfortunately none of the common species were found in Lake Turkana, but his results do indicate that there were few obvious seasonal trends. In Lake Chad, which is only 12-14°north of the equator, ROBINSON and ROBINSON (1971) found that there were sufficiently large fluctuations in the climate to cause significant seasonal differences. Maximum numbers were found in the 'hot' season and minimum numbers were found in the 'cold' season. The situation in Lake Turkana is somewhat different because local climatic conditions (see Chapter 1) are extremely stable. However, seasonal changes were detectable and associated with the annual flood from the River Omo. Maximum numbers were found in the northern part of the lake in March and August, and minimal numbers were found at the beginning of the flood season in July. The significant drop in the rotifer population at the beginning of the flood season is probably associated with the heavy silt load. MOGHABY (1977) describes the zooplankton of the Blue Nile, which has a similar discharge to the Omo River and also originates in the Ethiopian Highlands, a 'disappearing almost completely' during the flood season. He attributes this disappearance to the effects of the heavy silt load which clogs the respiratory and feeding apparatus of the zooplankters. Figure 3.35 indicates that contribution of the rotifera to the whole population increases further south in the Northern Sector during the flood season. However, the species diversity and the abundance remain relatively low.

The importance of the rotifera in the zooplankters of Lake Turkana in terms of their abundance and diversity is therefore unusually low, and their contribution to the production in open water is minimal. The exceptional area is the Northern basin and particularly the Omo Delta area where relatively high densities may provide an important food source to fish and to the predatory _Mesocyclops leuckarti_. The latter species is particularly abundant at a time when anadromous fish are congregating near the mouth of the River Omo prior to migrating up the river to spawn (see Chapter 9).

Crustacea

All species of this group are used as a prime food source by at least some stages of almost every fish species in the lake. A knowledge of their distribution and abundance is therefore very important in this study of the fishery potential.

There have been few detailed quantitative studies of the crustacean zooplankters in East African lakes. WORTHINGTON and RICARDO (1936) described the relative proportions and vertical distribution of zooplankton in several of these lakes including Lake Turkana. Since then, the work of BURGIS (1969, 1971, 1973 and 1974) on the distribution, abundance and production of zooplankton in Lake George, Uganda, and of GREEN (1967b and 1971) on the Cladocera in Lake Albert, are exceptional. RZOSKA (1976) has reviewed work on the Nile system and expresses surprise at the lack of intensive zooplankton studies on Lake Victoria. Detailed studies on other large Rift Valley lakes are also lacking, and little progress has been made since the descriptions of species (e.g. FRYER 1957 a, b, and c for Lake Malawi). Studies by ROBINSON and ROBINSON (1971), by GRAS (1969), and GRAS _et al_ (1967, 1971 and 1976) on Lake Chad, and by KALK (1976) on Lake Chilwa have provided a good deal of information on the zooplankton of large, shallow lakes in Africa.

The results of the distribution and abundance of zooplankton in Lake Turkana show that, as in most other African lakes, Crustacea are the dominant group. Protozoa were sometimes numerically dominant but never exceeded the crustacea in terms of biomass. Crustacea formed an average of 62.3% of the total numbers of zooplankters at the H1 site, compared with 35.1% protozoa and only 1.61% rotifers. Figure 3.37 shows the percentage number of crustacea at different sites along the mid-line of the lake in March, June and August. It is evident that a similar pattern existed throughout with a fall in the proportion of crustacea in the Central Sector resulting from an increase in the numbers of protozoa. The situation is more complex than Figure 3.37 suggests because the distribution and seasonal changes in abundance of the two main species, Tropodiaptomus banforanus and Mesoclycops leuckarti, differ. Figure 3.38 indicates a tendency for the proportion of T. banforanus to increase towards the south end of the lake while the converse was noted in Mesocyclops leuckarti with the highest percentage recorded near the Omo Delta (Fig. 3.39). The contribution of Thermocyclops hyalinus was more variable, with an increased proportion towards the south end in June, and absence from the North Sector and Omo Delta area in September (Fig. 3.40). The percentage number of Cladocera rarely exceeded 10% but Figure 3.41 indicates that their contribution to the total number of zooplankters was relatively constant with a general increase in March.

Comparisons with the zooplankton of other East African lakes are difficult becaused detailed studies are generally lacking. However, it is evident from the literture cited earlier that despite similar species compositions, the dominance and proportion of the species varies considerably. It is clear from the work of BURGIS (op. cit.) on Lake George that the Cladocera are scarce, but the dominant zooplankter was Thermocyclops hyalinus and there were no Calanoid copepods. RZOSKA (1975) indicates that Thermocyclops neglectus was the most common crustacean zooplankter in Lake Victoria but the combined totals of seven Cladoceran species made up 30% of the total numbers. WORTHINGTON and RICARDO (1936) showed that Mesocyclops leuckarti and Thermocyclops hyalinus formed 59% of the zooplankters in Lake Naivasha with the balance formed by Cladocera. The reasons for these differences in dominant species are not known but they probably reflect the availability of food sources. BURGIS (1973) has pointed out that the low proportion of filter feeding crustacea in Lake George, and the dominance of the raptorial phytophagous copepod Thermocyclops hyalinus, are probably related to the high densities of the blue-green algae Microcystis spp. which occurs abundantly in the lake. Thermocyclops hyalinus from Lake George have been shown to digest this alga (MORIATY et al, 1973). The dominant zooplankters from Lake Chad, Tropodiaptomus incognitus and Thermocyclops neglectus, are also species which ingest the dominant phytoplankter Anabaena sp., (GRAS et al, 1971). In Lake Turkana the algal densities are often very low in the open water (see Chapter 2, page 115) and do not therefore provide a reliable food source for the zooplankton. Thus, the dominance of Tropodiaptomus banforanus, illustrated by the results from site H1 in Figure 3.42, may be largely explained by its detrital diet. Gut analyses of copepodite and adult T. banforanus showed that in all cases undifferentiated detritus formed over 80% of the contents and that few recognisable algae were present. The inability of this species to digest Microcystis colonies can be deduced from intact cells found in faecal pellets. The reliability of the detritus as a food source was illustrated by the results obtained from sediment traps described in Chapter 1. These results indicated a relatively high proportion of particulate material in the water compared with temperate lakes, and although carbon analyses on the collected material were not possible, microscopic observations showed that it contained considerable amounts of organic detritus. The rapid utilisation of the organic component of the detritus is indicated by the very low carbon content (average 0.63%) found in the sediments by YURETICH (1976). Further evidence for the mainly detrital diet of Tropodiaptomus banforanus comes from a comparison of the changes in algal densities with those of this species at H1. It is evident that maximum concentrations of T.

banforanus generally occurred some time after peak abundances of *Microcystis* spp.

Figure 3.42 shows that the carnivorous cyclopod copepod *Mesocyclops leuckarti* was the second most abundant crustacean zooplankter at H1 with an average of 16.1% of the total. *Mesocyclops leuckarti* was first shown to be predominantly carnivorous in African lakes by FRYER (1957) who analysed the gut contents of specimens from Lake Malawi. GRAS *et al* (1971) subsequently confirmed this for Lake Chad populations and also found that the early copepodites were predominantly herbivorous, becoming increasingly carnivorous in their later stages. Observations on the gut contents of *M. leuckarti* from the open water of Lake Turkana showed that the chief items of prey of the later copepodite and adult stages were the nauplii of all copepod species and the copepodites of *T. banforanus*. Cladocera were also noted in the gut contents but no protozoa were observed. The inverse relationship between the proportions of *T. banforanus* and *M.leuckarti* at site H1 (Fig. 3.42) possibly indicates a relatively stable predator/prey system. Results obtained by WORTHINGTON and RICARDO (1936) indicate that the same species have dominated the zooplankton of Lake Turkana for at least 40 years.

The proportion of *Thermocyclops hyalinus* and Cladocera were relatively low throughout the year. Thus at site H1 *T. hyalinus* formed an average of 5.35% of the total number of zooplankters, and the proportion of Cladocera was even lower (4.3%). The comparative scarcity of these herbivorous forms was probably due to low algal densities. This is particularly true of the *T. hyalinus* population at site H1 which showed peaks in abundance coincident with those of the filamentous green alga *Planctonema lauterbornii* (see Chapter 2).

Other factors are also involved in determining the composition of the Lake Turkana zooplankton including predation, effects of relatively high salinity (direct or indirect) and the inflow of turbid water from the River Omo. The relationship between the distribution of copepods and the conductivity of the water in 48 East and Central African lakes has recently been described by LA BARBERA and KILHAM (1974). They conclude from this survey that the distribution of each species was limited to a range of conductivities in which they can maintain a viable population. The reasons for these limitations are not clear because, as LA BARBERA and KILHAM (*op. cit.*) point out, the effects of conductivity are not necessarily direct and may also depend on water chemistry. BAYLY (1967, 1969) for example has shown that some copepods in Australian lakes can maintain populations in high sodium chloride lakes but not in similarly concentrated sodium carbonate lakes. It is therefore possible to use copepods as indicators of specific water types. RUTTNER-KOLISKO (1971) used combinations of Rotifer species in a similar manner. It is probable that many species of copepods are excluded from Lake Turkana by high conductivity. LA BARBERA and KILHAM (*op. cit.*) indicate that many species were not found in lakes with conductivities above 2000 µS/cm k20 °C and conclude that biological interactions are more important below this level. It is interesting to note that although *Tropodiaptomus banforanus* was not found abundantly in any of the lakes studied by LA BARBERA and KILHAM (*op. cit.*), many of the species from Lake Turkana, including *Mesocyclops leuckarti*, *Thermocyclops emini*, *Microcylclops varicans* and *Afrocyclops gibsoni* were all found in a range of conductivities which exceeded or included that found in the open water (around 3400 µS/cm k25 °C).

The effects of predation pressure by pelagic fish such as Alestes baremose or A. minutus on the composition and size structure of the crustacean zooplankton are not clear. A full discussion of the effects will be given later (Chapter 10). However, surveys of pelagic fish indicate that the zooplanktivorous species A. minutus is particularly abundant near the west coast in the Central Sectors of the lake. Predation by this fish may well have caused the reduction in zooplankton concentrationson the west side of the sectors. The increase in the proportion of Tropodiaptomus banforanus towards the south end of the lake (Fig. 3.38) may be related to very low pelagic fish stocks in this region. There is surprisingly little change in the composition of the zooplankton in areas where pelagic fish stocks are higher. One might expect from BROOKS and DODSON's (1965) 'Size Efficiency' hypothesis to find an increase in the proportion of smaller filter feeders in these areas. However, a comparison between the composition of samples taken on the same day, in shallow water near the entrance to Ferguson's Gulf and in the middle of the lake, indicates that the composition was very similar despite an increase of predatory fish near the west shore. It seems likely that the smaller filter feeders do not, in this case, have a competitive advantage over the larger forms under conditions of increased predation. The salinity of the water and low algal production may well be the key factors.

The effects of inflowing turbid water from the Omo River were initially detrimental to all zooplankton populations, so that overall densities were reduced at the north end of the lake in July. The actual composition remained similar with the Crustacea making up 67.6% of the total numbers. The species least affected was Mesocyclops leuckarti, the adults and copepodites of which accounted for 29.13% of the total number compared with 12.3% in March of the same year. BROOK and PROUSE (1955) described a similar situation during the flood season on the Blue Nile where zooplankton disappears each year at the height of the flood. MOGHABY (1977) has indicated that populations regenerate from ephippia after the food has subsided and attributes the destruction of the zooplankton to a physical blocking of their feeding and respiratory apparatus by suspended solids. A similar situation probably occurs in Lake Turkana at the start of the flood season but no evidence of ephippia or resting eggs was found in zooplankton or mud samples. Results from the lakewide surveys show rapid recovery after the flood, presumably from surviving populations.

Figures 3.43, 1, 2 and 3 summarise the observed changes in total crustacean zooplankton densities in March, June and November. Although the number of sites used to construct these maps is relatively small, they illustrate important distributional features of the standing stock of zooplankton. It is evident that, with a few notable exceptions, the total crustacean densities remained between 1000 and 2500 x $10^4/m^2$ in the open water. In March densities in excess of 2500 x $10^4/m^2$ were found in the middle of the Northern Sector and on the east side of the Central Sector. Significantly low densities (less than 500 x $10^4/m^2$) were found near the west coast of the North and South Central Sectors, and relatively low numbers were found near the east side of the Southern Sector. However, standing stocks over most of the Southern Sector were relatively high. In June, densities were lower in almost all areas and although the lower concentrations near the Omo Delta were probably due to the effects of inflowing sediment, lower densities in the Central and Southern Sectors are less easily explained.

The results from December 1974 in Figure 3.43.3 show that stocks of zooplankton at the north end of the lake were greater than in June 1974 and suggest the re-establishment of non-flood populations under post-flood conditions. It is interesting to note that the west east gradient of decreasing zooplankton densities in the Central Sector noted in March 1973 was also evident in December. Results from the Southern Sector show that during December stocks were vey much lower than was the case in previous surveys, being generally less than 1000 x 10^4 /m^2. The reasons for this scarcity are not clear but, as pelagic fish stocks associated with the scattering layer in midwater are also low in the southern basin, food seems the most likely factor limiting zooplankton production in this area.

A comparison between the results for June 1973 with echo survey data (Chapter 8, Fig. 8.79) shows that the highest densities of zooplankton to the northwest of North Island coincide with heavy concentrations of pelagic fish. This may represent an area of unusually high productivity where zooplankton populations were maintained at high levels despite heavy predation.

Several factors may be involved in increasing densities of the zooplankton in the period December to March. Chapter 1 describes a lakewide increase in temperature at this time of year compared with subsequent months (Figs. 1.52 and 1.53) and a greater degree of mixing was noted (Fig. 1.47) which was caused by seasonally stronger winds (Fig. 1.33) blowing more regularly from the south east (Fig. 1.36). It will be seen later (page 200) that as with other crustacean zooplankton (e.g. ELSTER, 1954; BURGIS, 1970; SMYLY, 1974; GRAS and ST JEAN, 1969 and 1976) increased temperature results in a faster development rate for the eggs and probably also for later stages. GOPHEN (1976) has shown that all stages of Mesocyclops leuckarti from Lake Kinneret grow faster at higher tempertures and that clutch sizes increased with temperature from 15 ° to 22 °C. This was compensated for by a decrease in body size. In Lake Turkana, however, there was a small but significant decrease in the body size of copepodites and adults of Tropodiaptomus from north to south correlated with a decrease in temperature. It was also noticeable that the larger females produced more, but smaller, eggs. The increase in temperature would therefore result in a higher production rate.

The increased turbulence in March is also likely to result in a higher rate of zooplankton production, directly by re-suspension of detritus from the lake bed and shore, and indirectly by re-cycling nutrients for algal production.

The results also indicate that seasonal fluctuations in zooplankton densities in Lake Turkana are relatively minor compared with the situation found in temperate lakes (Figs. 3.43-44). The relative stability of zooplankton populations in equatorial African lakes where seasonal changes in climatic conditions are less marked was first demonstrated by BURGIS and WALKER (1972), who compared Loch Leven in Scotland with Lake George in Uganda. A comparison of the results from H1 in Lake Turkana with data from the open water of Lake George analysed by BURGIS (1969) shows that fluctuations are even less marked in Lake Turkana. Seasonality in zooplankton populations in Lake Turkana became more evident towards the north end of the lake with increasing influence of Omo River water.

Comparisons of total numbers of crustaceans with those of other East and Central African lakes are difficult because few quantitative studies have been carried out in the region. The results of BURGIS (1971) indicate that concentrations in Lake George are much greater, averaging approximately 1000 individuals/1 compared with 18.41/1 at H1 in Lake Turkana. Differences in areal densities are very much less because Lake George has a mean depth of 2 m (BURGIS op. cit.) compared with 31.2 m in Lake Turkana. The average areal density of crustacea at H1 was 14.7 x $10^5/m^2$ compared with 20.0 x $10^5/m^2$ in Lake George. Although summer populations of shallow, eutrophic, temperate lakes are much higher than comparable tropical lakes such as Lake George (BURGIS and WALKER, op. cit.), it appears from a review by WATSON (1974) of work on the Great Lakes of Canada that differences between zooplankton populations in deeper temperate lakes and those found in Lake Turkana are not so marked. Maximum and minimum concentrations from 30 stations on Lake Ontario range from 2 to 55/1, and a range of 2 to 24/1 was observed at a comparable number of stations on Lake Huron (WATSON op. cit.). During the present studies a strikingly similar range of 8 to 29/1 was noted at site H1 during 1973. The principal difference between temperate and tropical lakes is the lack of seasonality in the latter, particularly in equatorial situations. Reproduction in tropical zooplankton thus takes place continuously although not necessarily at a steady rate.

FERGUSON'S GULF

The evidence presented in Chapters 1 and 2 clearly shows that although not isolated from the main body of the lake, this area is physically different, has a very different algal population and a high rate of primary production. This unique combination of conditions has led to exceptionally high yields of Sarotherodon nilotica which has recently formed a very important part of the fishery (see Chapter 11).

Seasonal changes in the zooplankton population of Ferguson's Gulf were not investigated during the present study but the results shown (Fig. 3.45) for a survey of oblique hauls taken with the Clarke-Bumpus sampler are typical.

Mesocyclops leuckarti dominated the zooplankton of the dark green water in the Gulf. This is clearly shown (Fig. 3.45) by the results from sites 3 and 4 where the nauplii and later stages of this species made up over 95% of the total number of zooplankters. The two rotifer species, Brachionus dimidiatus and Brachionus plicatilis, Ostracods and a few Thermocyclops hyalinus were the only other zooplankters found in samples from the dark green Gulf waters.

In the north west (site 2) and near the entrance to the Gulf (site 1) where water from the main body of the lake enters by relatively strong wind generated currents, the zooplankton was more typical of that found elsewhere in the lake. In this region, distinguished by its lighter green colour (see Plate 1.2, Chapter 1), the algal species were a mixture of open water and inshore species. Here, Mesocyclops leuckarti copepodites and adults still made up between 20-26% of the total numbers, but Tropodiaptomus banforanus, Diaphanosoma excisum and Moina brachiata were found in similar proportions to those found elsewhere in the lake. Hexarthra jenkinae and Brachionus calciflorus were also found with B. plicatilis and B. caudatus in this region, forming a total of 9.63% of the total numbers of zooplankters at site 1, and 19.42% at site 2, compared with 1.04% at site 3.

The concentrations of the zooplankton species at sites 1 and 2 were similar to other inshore sites (e.g. Outer Buoy) with Tropodiaptomus banforanus found to be 88.7/l at site 1 and 130.0/l at site 2, and Mesocyclops leuckarti adults and copepodites 143.9 and 78.4/l at these two sites respectively. At the central site (site 3) Mesocyclops leuckarti was found at a concentration of 1378.0/l (3.45 x $10^6/m^2$) which was the highest density recorded for any species found in the lake. At site 4, however, although M. leuckarti was dominant, the total concentration of this species nauplii and later stages was only 159.7/l (7.9 x $10^4/m^2$) which was not exceptional. It is probably important to note that algal concentrations were also much lower at this site than at site 3.

The reasons for this spectacular change in zooplankton composition and for the very much higher concentrations of Mesocyclops leuckarti in the dark green water of the Gulf remain obscure. The two main factors most likely to be involved are, firstly, the much higher conductivity of the water ($< 4000\ \mu S/cm$ at k25°C : see Fig. 1.75, Chapter 1) and, secondly, the marked difference in algal composition. The reasons for the changes in algal composition and for the much higher rate of primary production in the Gulf have been discussed at length in Chapter 2. These factors almost certainly also cause an increase in secondary production. Examination of gut contents of Mesocyclops leuckarti from site 3 indicated that the younger stages were apparently feeding on the algae but, although the adults and later copepodite stages (C IV and C V) had ingested filaments of both Spirulina species and Anabaenba sp., they were apparently feeding mainly on their own nauplii, rotifers and other small invertebrates (Chironomids and Hydracarina). This may therefore provide an interesting case of cannibalism sustaining relatively high densities of later stages. It remains uncertain as to whether or not the later stages were digesting the algae because with densities of over 100 filaments/ml they would find some difficulty in avoiding them.

VERTICAL DISTRIBUTION AND MIGRATIONS

The vertical distribution and diel migrations of Lake Turkana zooplankton were first studied by WORTHINGTON and RICARDO (1936). The results clearly showed that in cases were precise identification was carried out, species tended to concentrate in a particular depth zone. An unusual situation was found where the dominant zooplankter Tropodiaptomus banforanus was concentrated near the surface in the afternoon and migrated downwards at night. Cases of reversed migration appear to be extremely rare in other lakes. In view of this exceptional situation a comprehensive survey of vertical distribution was carried out during the present study.

Sampling strategy

Methods used during the present study for collecting samples from each depth zone within the water column were described on page 165. The daytime vertical distribution of zooplankters was covered adequately by a vertical series of samples collected at each site during the course of lakewide cruises. Diel changes in vertical distribution were studied at site H1 on several occasions, and at a shallower site 1 km NW of Longech Spit. During these studies a series of vertical hauls was taken at 3 hourly intervals over a 24 hr period. Vertical distribution was also studied in detail during March 1975 at a series of seven daylight stations on a transect from Longech Spit to Allia Bay.

RESULTS

Vertical distribution during daylight

Under normal conditions the depths at which maximum densities of each species were found in open water were relatively constant. In view of this consistency, results from 96 series of samples have been summarised in Figs. 3.46, 47 and 49. These show the mean percentage occurrence of each species at different depths for samples taken between 10.00 and 16.00 hrs under calm conditions. Subtle features in the vertical distribution patterns are in some cases obscured by these summaries but the figures indicate depths at which maximum numbers are most likely to be found at this time of day. They also illustrate the vertical segregation of the zooplankton (Table 3.2).

One of the most interesting aspects of these results is that despite the very small variation in most of the physical parameters with depth, each species showed a different pattern in its vertical distribution. However, as one would expect from the general lack of stratification in the lake (Chapter 1) and the high degree of vertical mixing, none of the species was excluded from any depth. Viable populations of zooplankters were found in vertical hauls from the bottom ten metres throughout the lake, including the deepest area below the 110 m contour.

The common protozoans Raphidiophrys cf pallida and Vaginicola sp. nov. with their associated Vorticellids were normally the only species found abundantly in surface samples. Most of the horizontal hauls taken just below the surface contained very few other forms. This situation was not shown by the vertical hauls taken by WORTHINGTON and RICARDO (1936) but, as with the results of the present survey, they found maximum densities of Vaginicola sp. nov. in the top 5 m. A lack of detailed information precludes comparison with other East African lakes, but maximum concentration of Raphidiophrys sp. were found in the top 5 m of Lake Edward and Lake Naivasha by WORTHINGTON and RICARDO (1936).

Rotifers were generally scarce but Figure 3.47 shows that highest concentrations were normally found in the top 10 m, with Hexarthra jenkinae more common at greater depths than Brachionus plicatilis or Felinia terminalis. Both RUTTNER-KOLISKO (1974) and ELLIOTT (1977) found that some species of Rotifers had a definite pattern in their vertical distribution in unstratified conditions in temperate lakes. The former author concluded that this was due to a definite vertical migration in response to light. In view of the very small variation in the other physical parameters measured in Lake Turkana, the results from the present survey would support this view. However, the results from two sites at the north end of the lake illustrated in Figure 3.48 indicate that considerable modifications to the vertical distribution pattern of the rotifers occurred during the inflow of turbid water from the Omo River, even when the river is not in flood. Surface conductivity at the most northerly site (10 km due south of the Omo Delta) was lowered by the inflow of fresh water. Under these conditions of reduced light penetration both Hexarthra jenkinae and Brachionus plicatilis were found deeper than at the site 20 km due south of the Omo Delta which was not influenced by the inflowing water. It is also evident that the number of species found nearer the Omo Delta was much greater. This situation has been discussed previously (page 172).

The vertical distribution of the copepodites and adults of the three common copepods and the most common cladoceran are illustrated in Figure 3.49. The results are similar to those of WORTHINGTON and RICARDO (1936) except that differences in the vertical distribution of the two cyclopoid copepods are shown. These were not separated to species level in the earlier study. Descriptions of the vertical distribution and migrations of planktonic crustacea in temperate waters are numerous but there are few records from East or Central African lakes. In most temperate lakes planktonic crustacea are found at deeper levels during the day (e.g. WETZEL, 1975) but the results from Lake Turkana show that Tropodiaptomus banforanus was most abundant near the surface. It is interesting to note that WORTHINGTON and RICARDO (op. cit.) also found that the crustacean zooplankton of Lake Edward and Lake Bunyoni were concentrated in the upper layer during the daytime. Metadiaptomus aethiopicus males were found at slightly deeper levels in Lake Bunyoni at night.

The only Cladoceran found in sufficient numbers to plot its vertical distribution in this manner was Diaphanosoma excisum. Maximum concentrations were normally situated below the copepods and the species rarely occurred abundantly near the surface. Moina brachiata, Ceriodaphnia rigaudi and Hyalodaphnia barbata were all found in relatively small numbers, but the mean depths at which maximum numbers were found (Table 3.3) indicate that they were usually found most abundantly at similar depths to Thermocyclops hyalinus.

Figures 3.51-62 show the vertical distribution of each species found on a transect from Longech Spit to Allia Bay (see Fig. 3.50). The figures serve to illustrate the variation normally encountered in each species.

The results for the two common Protozoa indicate that they were not always found in maximum concentrations near the surface and that although Raphiodophrys cf pallida normally declined at depths greater than 40 m, relatively high numbers occurred between 40 and 60 m at site 5. The concentrations of Gyratrix hermaphroditus were low but indicated relatively high densities in mid-water.

Figure 3.55 a, b and c show that Tropodiaptomus banforanus adults and copepodites were found mostly in the top 10 m but that nauplii were more evenly distributed throughthe water column although in mid-lake they were less common. Figure 3.56 indicates that after metamorphosis from naupliar stages the copepodites migrate towards the surface and that during subsequent instars no further change in the distribution pattern occurs until the attainment of maturity. The results suggest that in adult T. banforanus the tendency to concentrateon the surface is greater than in copepodites (Fig. 3.55). A slight but persistent reduction in numbers in the 10-20 m depth zone is evident in adults at both sites, and in late copepodite stages at site 4 (Fig. 3.56). The midwater scattering layer formed chiefly of the planktivorous Alestes minutus was situated at the same depth and the lower densities of T. banforanus may be due to predation. It is interesting to note that on the same transect the vertical distributions of Engraulicypris stellae and the prawns Macrobrachium niloticus and Caridina nilotica were also interrupted in a similar way with relatively low numbers between 10 and 20 m (see Chapter 8, Fig. 8.45).

Adults of Mesocyclops leuckarti (Fig. 3.57 a) were also most abundant near the surface but the copepodite stages (Fig. 3.57 b) showed less tendency to concentrate in the top 10 m. As in the late stages of T. banforanus, the number of adult M. leuckarti was relatively low in the 10-20 m depth zone at sites 4 and 5.

Copepodites and adults of Thermocyclops hyalinus were found most abundantly at lower levels than the two other copepods. The results (Fig. 3.58) indicate that the distribution was similar for both adults and copepods. This species was found commonly in the top 10 m only near the shore.

Concentrations of Cladocera were generally low but Figures 3.59-62 show a considerable variation in vertical distribution. It is evident that in open water they were most abundant between the 10 and 20 m depth zone but inshore reltively high concentrations were recorded in the surface layers.

Vertical migration

Results from 24-hour studies

Results from 24-hour studies at H1 and at a site 2.5 km off Longech Spit showed that a distinct vertical migration occurred in several species of crustacean zooplankton. Sampling depth intervals were usually too large to detect any movement of protozoa and rotifera.

Examples of crustacean movements observed at the two sites are shown in Figures 3.63-66. The results confirm the findings of WORTHINGTON and RICARDO (1936) for Tropodiaptomus banforanus and Diaphanosoma excisum and provide new information for the two cyclopod copepods which were not separated in the earlier study. At H1 maximum numbers of adults and copepodites of T. banforanus were found in the surface layers until 23.30 hrs but by 07.00 hrs the population peak had moved downwards to lie between 5 and 15 m where they remained until after 10.00 hrs. A very similar reversed vertical migration was observed at the Longech station. Diaphanosoma excisum was not found in sufficient numbers at H1 to plot its vertical migration but the results from Longech Spit (Fig. 3.36 b) indicate a normal vertical migration with a distinct movement towards the surface between 16.00 and 19.00 hrs and descent by 06.00 hrs.

Figure 3.65 shows that Thermocyclops hyalinus also had a normal vertical migration with maximum numbers situated at 35-45 m during daylight rising to the surface layers by 22.30 hrs. The distance moved by this species, at a rate of about 3 m/hr, is remarkable considering the low transparency of the water. Mesocyclops leuckarti copepodites and adults showed a reversed migration pattern resembling that of T. banforanus with maximum numbers near the surface during the day (Fig. 3.66). The patterns, however, differed in detail with M. leuckarti descending from the surface earlier in the night than T. banforanus, although both species moved down to similar depths. The adaptability of M. leuckarti to local environmental conditions is amply demonstrated by this movement. Under normal conditions this species migrates to the surface at night (e.g. BEGG, 1976) but in a shallow eutrophic lake (Esthwaite) in the English Lake District, SMYLY (1961) found no detectable vertical migration. In Lake Turkana the reversed vertical migration of M. leuckarti is probably associated with its role as a predator of Tropodiaptomus banforanus.

Results from vertical hauls over 24 hrs did not reveal any vertical migrations of the protozoa or rotifera. In the latter case this was due to the low concentration. Results from horizontal hauls taken during the day shown in Figure 3.67 show a distinct movement for Raphidiophrys cf pallida towards the surface in the middle of the day, and away from the surface in the afternoon. This movement is similar to that found for some algal species in Lake Turkana (see Chapter 2). The very few studies which have been carried out on vertical migrations of protozoa (e.g. GOULDER, 1972 for ciliates in a shallow eutrophic lake in England) have not shown any vertical migrations of this type.

Similar results for the two common rotifer species Hexarthra mira and Brachionus plicatilis (Figs. 3.68 and 3.69) also show differences in vertical distribution during the day. B. plicatilis moves close to the surface at 11.00 hrs and descends to between 10-15 m late in the afternoon. Hexarthra mira on the other hand was most abundant between 10 and 15 m for most of the day and moved upwards later in the day.

DISCUSSION

The vertical migration of planktonic crustacea in fresh and salt water has attracted a great deal of attention. The resulting extensive literature has been reviewed by CUSHING (1951), HARDY (1956), WYNNE-EDWARDS (1962), McLAREN (1962) and KERFOOT (1970) who comment on the various theories used to interpret the observed phenomenom, and extend the ideas by formulating general models to explain the adaptive value of the movements.

In Lake Turkana, a knowledge of the movements of the zooplankton is important for the estimation of production rates, firstly because the development time of at least the egg stages is primarily dependent on temperature which varies with depth, and secondly because changes in vertical distribution affect their availability to predatory fish. It will be seen later (Chapter 8) that such fish are often associated with the midwater scattering layer which also undergoes marked diel vertical migrations strongly correlated with light penetration (see Chapter 1, Fig. 1.88).

Although the results from 24 hr studies on Lake Turkana showed definite vertical migrations, the depths at which most species were found in maximum concentrations during the day varied considerably. Thus the copedodites and adults of Tropodiaptomus banforanus were not always found near the surface during the afternoon. For this reason, the results of vertical distribution studies for the most abundant zooplankter T. banforanus were investigated in more detail, in relation to physical factors recorded at each site and to the position of the scattering layer. Data for this analysis were available for 45 separate series of observations, 12 from H1 and the rest from lakewide cruises. The following parameters were used:-

L = Light penetration: the recorded light intensity at 3 m in using a clear glass filter

T = Time: time of day East African Time (EAT)

WT = Temperature: the surface temperature in C was used. Surface temperatures were chosen because fluctuations were greater than elsewhere in the water column, although small compared with temperate climates. It has been shown in Chapter 1 that changes at the surface reflect minor but nevertheless detectable changes at deeper levels.

D = Depth: The depth of water at the site in metres

WD = Wind strength: recorded on the Beaufort scale (0-8)

S = Sea state: on a scale from 0-6 estimated by the master of the research vessel

SCAT = Scattering layer depth : distance in metres from the surface to the middle of the midwater scattering layer.

MN = Mean depth at which maximum numbers of *Tropodiaptomus banforanus* copepodites and adults were found at each site in metres.

DX = Dispersion index of *T. banforanus*: the variance of the above mean.

There was insufficient data to include oxygen concentration or conductivity, but the former was strongly correlated with temperature, and the latter varied very little at the sites used. Food availability in the form of bacterial detritus may also have been important but no data were available on the vertical distribution of this factor.

It was evident from the data matrix formed from these factors (see Table 3.3) that a multivariate analysis technique would provide an effective method of ordination to rationalise the position of MN in relation to the prevailing physical factors. A principal components analysis (PCA) was used to reduce the data to reasonable dimensions. The statistical package used for this analysis was ASCOP at the Atlas Computer Laboratory (COOPER, 1972). Other, and according to GAUCH *et al* (1977) more accurate ordination techniques, such as polar ordination or reciprocal averaging, are available, but as will be seen later the PCA proved to be very useful in helping to interpret the results.

The basis of PCA has been described by KENDAL (1957), and its uses by many authors including JEFFERS (1967) and ORLOCI (1975). In this case the analysis was performed on a matrix of correlation coefficients of log transformed regressions between each set of variables (Analyses carried out on the variance - co-variance matrix gave similar results). Each component calculated is orthogonal and accounts for successively less variance. The eigenvalues extracted from the matrix of correlation coefficients incidate the amount of variance accounted for by each component, and the eigenvectors show the extent to which each variable has been used to define the dimension. Each site has a score on each component and has a unique position on a bivariate plot of scores on two components. The distance between the sites on the plot gives a measure of similarity between the results obtained at the sites.

Cluster analysis can be used to quantify these similarities (see e.g. SPRULES, 1977, for zooplankton communities in different lakes) but it will be seen (Fig. 3.70) that sites were insufficiently clustered to warrant using this type of technique. In this case the PCA results were used to indicate general trends in the effects of variables on the depth and degree of dispersion of Tropodiaptomus banforanus adults and copepodites.

The matrix shown in Table 3.4 indicates that there was some degree of correlation between variables. In particular the negative correlation between water temperature, wind and sea which must be borne in mind when interpreting the results. The degree of correlation between variables was expressed in a PCA carried out with MN and DX excluded, i.e. just the physical factors. The first component of this analysis was formed from roughly equal proportions of sea state, wind, water temperature and light, the second from depth, and the third almost exclusively from time.

A PCA with all variables MN, DX and SCAT gave some illuminating results. Table 3.5 indicates that over 83% of the total variance was accounted for by the first three components (PC1, PC2 and PC3). Table 3.6 shows the component coefficients (eigenvectors) which indicate the extent to which the variables acted to produce the component. The table also shows the correlation of the variables with these two components. The results from PC1 indicate that the depth at which maximum numbers of Tropodiaptomus banforanus were found, increase as:

(a) Light penetration increases

(b) The sea state increases

(c) The depths of the site increases

(d) The depth of the midwater scattering layer increases

(e) The water temperature at the surface decreases

(f) Time decreases (i.e. move up as time progresses during the day)

The results also indicate that they become more dispersed as they descend. The correlation of most of the variables with PC2 is low but indicates that water temperature and depth decrease as the wind increases. This result is reasonable because the deepest part of the lake (the south end) is also the windiest (see Chapter 1).

The ordination produced by a bivariate plot of the site scores on PC1 and PC2 is shown in Figure 3.70. This ordination groups sites where similar conditions prevailed, and separates groups of sites where extremes of conditions were found further from the centre. For example sites 1, 3 , 10 and 15 were the only sites with a completely calm sea and 43, 45 and 42 were sites where light penetration was deepest. A comparison of the ordination with the original data shows that deep MN values are associated with heavy seas and maximum values for light intensity. The former is illustrated in Figure 3.71 which shows the positive correlation found between MN and sea state when the results from 3 shallow sites (30, 34 and 35) are excluded.

One can conclude from the results that, despite the obvious reversed diel migration found in 24 hr studies for Tropodiaptomus banforanus (Fig. 3.64) the sea state and light intensity act independently to modify the migration.

The rise in wind speed and resulting increase in sea state probably provide the main stimulus for the movement of adults and copepodites of T. banforanus away from the surface at night. It has been seen earlier (Chapter 1, Fig. 1.38) that a very striking pattern in wind speed was found at Lake Turkana, with strong winds often starting before dawn and persisting through the morning. The downward movement of T. banforanus after midnight and before dawn at a time when wind and sea increased is well illustrated in Figure 3.63. Their return to the surface in the afternoon is associated with calm conditions. As was noted in Chapter 1 (page 28) in the study of this diel wind pattern, calm conditions prevailed on 82.7% of the afternoons between 16.00 and 20.00 hrs, and wind speeds decreased normally after 13.00 hrs. As they moved down after midnight, light is unlikely to be used as a reference for the descent. However, it is evident from the results that T. banforanus adults and copepodites were not found close to the surface in clear water during the day as they were in more turbid conditions. It seems likely that they use light as a more general reference point to which their reaction is slower. Evidence for the lack of rapid reaction of T. banforanus to steady short-term changes in light intensity was obtained from a series of vertical hauls at different depth intervals taken before and after the total eclipse of the sun at 16.00 hrs on 30th June 1973. The results show that unlike the fish (see Chapter 8) T. banforanus did not respond to reduced light intensity during the eclipse.

The most important result of the downward movement of T. banforanus adults and copepodites at the onset of windy conditions is that they reduce their exposure to rapid lateral displacement by wind-generated surface currents. It has been shown in Chapter 1 that large volumes of water are moved in a north westerly direction by the strong prevailing south easterly winds to a depth of over 6 m. Lateral displacement of surface dwelling Cladocera by wind generated currents has been demonstrated by GEORGE and EDWARDS (1976) in a small temperate lake where the wind pattern was much less predictable than at Lake Turkana. During the present investigations, the inverse relationship between densities of pelagic fish and T. banforanus, particularly in the Central Sector, suggests that the copepod successfully avoided lateral displacement. However, the dense concentrations of pelagic fish near the west coast (see Chapter 8) are thought to rely on the constant replenishment of food resources by the transport of zooplankton into the area by wind generated surface currents. It is therefore probable that the low densities of T. banforanus observed near the west coast were in fact due to heavy predation by fish.

We cannot be certain that the effect of rough seas is a direct, physical effect or an indirect effect, because an increase in wind speed is associated with a decrease in temperature near the surface. The relationship with temperature is less obvious from the results of PCA, but the descent of adults and copepodites from the surface at night when the surface waters cool (see Figs. 3.63 and 3.64), and during the day when the lake is rough, suggest that the reaction also avoids lower temperatures. It will be seen later that a drop in water temperature of 1 °C results in an increase in egg development time of around 9 hrs from 1.2 to 1.6 days, and would thus result in a decrease in the rate of recruitment to the population. The adaptive value of vertical migration with respect to temperature has been discussed in length by McLAREN (1962). His model is based on the inverse relationship between fecundity and temperature and the positive correlations between growth, feeding and temperature. He suggests that vertical migration results in exposure to fluctuating temperature environments, thus optimising the balance between growth and fecundity. Unfortunately, diel feeding patterns for *Tropodiaptomus banforanus* in Lake Turkana were not established, but the results are apparently not in agreement with this model. However, DIGBY's (1961) results from arctic waters with 24 hrs daylight show that *Calanus* species and *Sagitta* species stayed near the surface (between 1-10 m) and showed only a very slight vertical migration. McLAREN (*op. cit.*) argues that temperature fluctuations under these conditions may not be great enough for vertical migrations to be advantageous with respect to his fecundity/growth model. The same argument could be applied to the conditions in Lake Turkana. DIGBY (1961) also found that migration was most pronounced at the most sheltered of his sites where thermal stratification would be greatest.

KERFOOT's (1970) model ignores the effects of temperature and concentrates on light intensity productivity, time, and the depth of the populations. He concludes that light intensity is usually used as a reference point for positioning the zooplankton in relation to maximum benefit from producers. Unfortunately no data are available on the depth distribution of the food of *T. banforanus*, but the strong positive correlation between light intensity at 3 m and the depth preference of this species suggest that light intensity is used as a reference in a rather unusual way. Under relatively calm conditions they migrate upwards to a specific diurnal level of light intensity whereas most species tend to follow a particular isolume downwards.

Another and probably important result of the migration is that they avoid predatory fish, particularly *A. minutus*, associated with the scattering layer for much of the time. The results of the PCA show that the movements are in the same direction but there is no direct correlation between the scattering layer depth and MN. In most cases the scattering layer depth was above MN between 09.00 and 12.00 hrs, and below MN between 12.00 and 14.00 hrs. There were only 10 records from the 43 used here where scattering layer depth was within 1 m of MN. It would seem therefore that vertical migrations effectively reduce their exposure to some predatory fish. This situation is analogous to the migrations of zooplankton and fish in Lake Kariba described by BEGG (1976). Here the migrations are again inversely related, with *Mesocyclops leuckarti* and *Bosmina longirostris* showing a normal vertical migration while their main predator, *Limnothrissa miodon*, was shown in echo traces to have a reversed vertical migration.

The comparatively low numbers of other zooplankton species precluded extensive analysis of the factors affecting their vertical distribution, but the results presented earlier show that *Mesocyclops leuckarti* underwent a limited reversed vertical migration. This was in marked contrast to the Lake Kariba population (BEGG, 1976) where *M. leuckarti* followed a normal pattern of diel migration. The competitive advantage of the reversed pattern in Lake Turkana was probably associated with maximising fecundity and growth rates and with the predation of this species on the copepodites of *Tropodiaptomus banforanus*.

Thermocyclops hyalinus and *Diaphanosoma excisum* exhibited a normal vertical migration and were usually found at deeper levels.

PRODUCTION

Introduction

The preceding sections of this chapter have described the distribution and abundance of the zooplankton. Estimates of production rates are equally important for assessing the fishery potential of the lake. This section describes calculations of zooplankton production which have been largely concentrated on the most abundant zooplankton species, Tropodiaptomus banforanus.

Two methods, based on the concept of the balance between renewal and elimination, put forward by ELSTER (1954), have been used to calculate net production rate. In Lake Turkana where eggs are produced all year, the processes are continuous and the populations remained relatively steady. The first method assumes an absolutely steady state in the populations and is based on calculating the turnover time (T) of STROSS et al (1961) from the birth rate. The latter calculations are based on work by EDMONDSON (1968) on continuous reproduction in rotifer populations and has been used by BURGIS (1971) for calculating production rates of Thermocyclops hyalinus in Lake George, Uganda. The second method calculates the net production of each stage and is an elaboration of methods devised by WINBERG et al (1965) and HILLBRIGHT-ILKOWSKA and PATALAS (1967). This requires a knowledge of specific growth rates and is thus more complex but has less demanding constraints.

Calculation of net production based on turnover time (T)

The basis of this method is relatively straightforward and requires a knowledge of the following parameters:

(i)	Population density per unit volume	- No
(ii)	Clutch size (eggs/female)	- E
(iii)	The number of females carrying eggs per unit volume	- F
(iv)	The egg development time in days	- D_e
(v)	Population weight per individual	- W
(vi)	Biomass per unit volume	- (No x W)

The method assumes that net production per day is equivalent to the proportion of the population replaced each day in order for it to remain steady. This is calculated from the turnover time (T) which is the number of days the population takes to replace itself from neonates.

i.e. Net production = $\frac{No \times W}{T}$ in wt/unit vol/day

where T is the unit of time used (1 day) divided by the finite birth rate B' where B' = $\frac{eggs/l/day}{No}$

The number of eggs hatching per litre per day (E') calculated from

$$E' = \frac{E \times F}{D_e}$$

Under the strict constraints of continuous mortality and natality this method gives a relatively accurate estimate of production. However, as will be seen later, this is rarely the case even under conditions as steady as those found in Lake Turkana, and is therefore an approximate estimate of the actual net production.

The only parameters not so far described are the egg development time (D_e), the number of eggs per litre, and biomass.

Egg development time (D_e)

ELSTER (1954) has shown that the rate of development of copepod eggs is primarily dependent on temperature. Two methods were used to calculate D during the present study, the first of which is almost identical to that used by BURGIS (1976), based on the method described by TAUBE (1966). It assumes that as egg production is continuous, a random selection of females carry eggs at different stages of development. The time taken for all the eggs to hatch from these females is therefore very close to the total egg development time. If the number of females carrying eggs (or embryos) is plotted against time, D_e is given by the point where the regression line meets the time axis (Fig. 3.72).

Samples for these experiments were collected at about 06.30 hrs from open water just north of Longech Spit near the 'Outer Buoy'. On each occasion a zooplankton sample was collected with a Plymouth tow net with large water samples (ca 201). The zooplankton was washed into one of the water samples prior to transportation to the laboratory. Females carrying eggs were removed from the sample under a low power binocular microscope and each placed in a separate phial containing 20 mls of filtered lake water. The lake water had been filtered through metal filter of 10μ aperture size, thus removing all crustacean zooplankton, eggs, and large clumps of algae. The phials were then placed in a constant temperature bath in the dark, and observed after one hour and then every two hours until all the eggs had hatched. In the case of Tropodiaptomus banforanus the eggs were in sufficiently small numbers (up to a maximum of 8 per female) to be counted at the beginning of each experiment. The number of females with eggs used in each experiment depended on availability and time, but normally they were sufficiently abundant to obtain between 40 and 60. In most instances the experiments were started about 1-2 hrs after the animals were collected.

Results of the experiments are shown in Table 3.7 which indicates mean egg development times for each species over a relatively narrow range of temperatures. The range of temperatures used for Tropodiaptomus banforanus was still greater than the maximum range found in the lake (see Chapter 1). The table also shows results from Thermocyclops hyalinus and Mesocyclops leuckarti from other lakes within the same range of temperatures. It is evident from a comparison of results for egg development times of Mesocyclops leuckarti that significant differences are found in lakes with divergent temperature regimes. In temperate climates, the development rate at 20°C obtained by TAUBE (1966), EINSLE (1968) and SMYLY (1974) was similar to the rate observed at 22°C in Lake Chad by GRAS and SAINT JEAN (1969 and 1976). An even lower rate was noted in Lake Turkana during the present study at comparable temperatures (81 hrs at 20°C and 66.5 hrs at 22° C). It is concluded that the development rate tends to vary inversely with the mean ambient temperature of different lakes. This adaptation may have evolved through a necessity for natural regulation of populations of M. leuckarti by conservation of the available energy for egg production by virtue of their reduced size in comparison with slower growing 'winter' populations.

The results also show that the egg development time of T. banforanus decreases in a non-linear manner with increasing temperature. This decrease differs from most species. SMYLY (1974) was able to fit egg development times of three copepods on a Belehradek's function where $D_e = a(T-\alpha)^b$ where T is temperature in C and a, α and b are constants. He was therefore able to extrapolate for D_e at different temperatures. This type of curve could not be used for T. banforanus because D_e decreases very much more quickly above 25 C and increases after 27.5 °C as shown in Figure 3.73. It is also evident that there were insufficient data for the other species to fit this type of function. Values of D_e for intermediate temperatures were therefore extrapolated from Figure 3.73.

The second method of estimating egg development time was more direct and was used only for Tropodiaptomus banforanus. Adult females without eggs were removed from the samples obtained for the indirect method and placed in phials containing 20 ml of filtered lake water with mature males. The females selected were those ready to produce eggs with well developed green fat bodies. Mature males were more difficult to distinguish since they showed no tendency to accumulate fat before mating. The phials containing the pairs of adults were then transferred to a constant temperature bath and observed every two hours. Notes were made on the time of mating, egg production, egg number and hatching. The estimates of egg development time presented in Table 3.8 serve to confirm the indirect determinations shown in Figure 3.73. Since observations in the direct method experiments were made at two hourly intervals, the errors were greater than in the case of the indirect method, and in consequence results for the latter were used in production calculations.

Experiments using the direct method provided information on mating success and on the timing of egg production. Results from all observations where egg production was successful have been combined in Table 3.9 and it is clear that the process is continuous throughout 24 hrs proving that the assumption made for the indirect method of determining egg development time is valid.

It was also found that in most cases pairs were successful in producing eggs within a relatively short time period. This is illustrated by the results from one experiment carried out at 30°C using 50 pairs over a period of 54 hrs. Of these pairs:

(1) 29 produced eggs which hatched in a mean development time of 38.4 hrs

(2) In 11 cases one or both adults died before eggs were produced

(3) 10 pairs lived for 54 hrs without producing eggs

(4) None produced a second batch of eggs

The egg production success rate was similar in most of the other experiments, but no pairs produced eggs at 35°C and a high proportion (60%) died within 38 hrs.

Clutch size (E) and the number of females carrying eggs per litre (F_e)

As the errors of estimating clutch size and the number of females carrying eggs from routine zooplankton counts were relatively large (ca 50%), these parameters had to be re-calculated using a larger number of counts. The mean clutch size and the percentage of female *T. banforanus* carrying eggs was therefore calculated from batches of fifty ovigerous females derived from routine zooplankton samples collected during the experimental period. This reduced the error of the estimate of the proportion of ovigerous females in the population to ±20% assuming random distribution in the sub-samples. The error on the estimate of clutch size is very much less for *T. banforanus* since the number of eggs in a clutch rarely exceeded four.

Errors due to clutches becoming detached from females during collection, preservation and sub-sampling were also possible. However, very few loose eggs of *Tropodiaptomus banforanus* were observed during counts. This source of error probably resulted in only a slight underestimate of production rates.

RESULTS

Production of Tropodiaptomus banforanus at H1 and the Outer Buoy site

Results of production calculations for *T. banforanus* using the egg development time method on eight occasions at site H1, and on five occasions at the Outer Buoy site, are shown in Tables 3.10 and 3.11 respectively. These indicate a mean rate of 0.00103 $g/m^3/day$(0.0828 $g/m^2/day$) at H1, and 0.0480 $g/m^3/day$ (0.5280 $g/m^2/day$) at the inshore site. The maximum range from all the estimates was from 0.097 $g/m^3/day$ at the Outer Buoy site on 27th March 1974 to 0.00038 g/m^3 /day at H1 on 19th February 1973.

Production calculations for Tropodiaptomus banforanus based on specific growth rates

This method, which requires a knowledge of the development times of each stage of the copepod life cycle, is based on the work of WINBERG *et al* (1965) and HILLBRIGHT-ILKOWSKA (1967). The daily production rate for each stage is described by the general statement

$$\text{Net production per day} \qquad P = \frac{(W_b - W_a) \times Na}{D_a}$$

for stage a to stage b, i.e. The number of individuals of a particular stage passing to the next stage in a day, times the difference in mean biomass of the individuals in each stage.

When this is applied to the whole population and to egg production, the complete equation (for symbols see Table 3.12) is as follows:-

$$P = \frac{(W_e \times N_e}{D_e} + \frac{(W_n - W_e) \times N_e}{D_e} + \frac{(W_{CI} - W_n) \times N_n}{D_n} \ldots \frac{W_{Ad} - W_{CV}) \times N_{CV}}{D_{CV}}$$

This gives net production per day, and in the method used by WINBERG *et al* (1965) the daily production rate is multiplied by the number of days between sampling to give an estimate of production for the period in question.

The method may be refined by taking into account the constant change in age structure on a daily basis and calculating the production for each day between sampling dates. This is based on the initial age structure found in the sample on day 1 and caclulations of the expected new structure on the following day from

$$\text{Nb on day 2} = \text{Nb on day 1} - \frac{\text{Nb on day 1}}{D_b} + \frac{\text{Na on day 1}}{D_a}$$

where a and b are distinguishable stages with known development times. If this is applied to all the stages, net production calculated by the method of WINBERG et al (1965) is the sum of the product of each stage. At the same time, the expected structure for the following day is calculated. The procedure is then repeated for day 3 and so on. The general scheme is then:

Day 1	**Day 2**	**Day 3**
E'_1	E'_2	E'_3
Nn_1	$Nn_2 = Nn_1 - \frac{Nn_1}{D_n} + \frac{E'_1}{D_e}$	$Nn_3 = Nn_2 - \frac{Nn_2}{D_n} + \frac{E'_2}{D_e}$
NCI_1	$NCI_2 = NCII_1 - \frac{NCII_1}{D_{CII}} + \frac{Nn_1}{D_n}$	⋮
$NCII_1$	⋮	etc
$NCIII_1$	⋮	⋮
$NCIV_1$	etc	⋮
NCV_1	⋮	⋮
NAd_1	$NAd_2 = NAd_1 + \frac{NCV_1}{D_{CV}}$	$NAd_3 = NAd_2 + \frac{NCV_2}{D_{CV}}$

where E' = Eggs/l, n = nauplii, CI-VC = copepodite stages I to V, Ad = Adults, N = Number per litre and D = Development time in days.

The input to the system in terms of eggs hatching per litre (E') can be calculated from

$$E' = \frac{\text{\% Adults carrying eggs (\%AdE)} \times \text{Clutch size (E)}}{D_e}$$

however it was obvious from the samples that both these parameters (%AdE and E) changed from one sampling day to the next. This can be partially accounted for by introducing a daily change so that the number of eggs hatching on day 2 (E'_2) is

$$E'_2 = \frac{\frac{NAd_2}{100} \times E_1 + \frac{E_n - E_1}{n} \times \%AdE_1 + \frac{\%AdE_n - \%AdE_1}{n}}{D_e}$$

where n is the number of days between samples. Such a procedure did not account for a sudden change in either parameter. It seemed most likely, however, that a change of this type would be gradual.

The number of changes for each stage over n days between samples was summated and multiplied by the mean change in biomass between that stage and the next to give a total net production between sampling days. It was also interesting to compare the observed structure of the population with the expected one calculated from the previous sampling date. PETROVICH et al (1961) used this difference to calculate production by loss (.e.e expected-observed) but WINBERG is quoted by SMYLY (1973) as believing the 'loss' method to be less accurate.

The concentration and specific growth rates of each stage were required for this method.

Instar analysis

Eggs, nauplii and adults of Tropodiaptomus banforanus were readily distinguished but instar analysis of copepodite stages was more difficult and was carried out separately. It was found that total body length measurements of the copepodites gave clearly separated polymodal frequency distributions with each peak corresponding to a different stage. Results from two examples of this type of analysis are shown in Figures 3.73-74. These illustrate the separation of copepodites and the distinct difference in sizes which were found between samples. The results also gave length frequency distributions for calculating biomass.

Results of mean body length measurements of copepodites and adults from the 'Outer Buoy' and site H1 samples used in production calculations are shown in Figures 3.75-76. These illustrate the small but often significant (see Fig. 3.77) differences in body length found on different sampling days. In view of these differences, mean body lengths from between sampling days were used to calculate mean weights for each stage in production estimates. Since failities for accurate determination of weight relationships were not available at Lake Turkana the expression $W^{-3} = 0.34L - 0.03$ (where W = wet weight in mg and L = length in mm) from EDMONDSON and WINBER (1971) was used and converted to dry weight by applying a factor of 20%, following BURGIS (1971).

Development time of post-egg stages

The development time of later stages was observed from laboratory experiments, and to a lesser extent from following growth cohorts shown by instar analysis.

Laboratory observations

The development rates of nauplii and copodites were estimated by observing the growth of individuals produced from the egg development time experiments (see page 201). Nauplii produced during these experiments were individually placed in phials containing 20 mls of filtered lake water and observed every two hours for the first day and subsequently as frequently as possible. The water in the tubes was maintained at a constant temperature and changed every two days. Although Tropodiaptomus banforanus was successfully reared to maturity, eggs were never produced under these experimental conditions.

Despite apparently constant conditions, the time taken to reach the adult stage varied considerably. Variations in development time were most marked in the later stages. Results from the observations are shown in Table 3.13 which indicates the mean development time for each stage to the nearest 0.5 days at 27°C in the case of the site H1 calculations, and at 29° C for the Outer Buoy samples. It is interesting to note that the development times used for the H1 samples were similar to those found by GRAS (1970) for Tropodiaptomus incognetus in Lake Chad, but slower than values reported for temperate calanoids at lower temperatures. For example, GEILING and CAMPBELL (1972) found that the total development time for Diaptomus pallidus copepodite stages was only 14.6 days at 25° C compared with 21 days for T. banforanus copepodites in Lake Turkana at 27°C. Temperature is not the only factor to affect growth rates of diaptomids. CORKETT and McLAREN (1971) have clearly shown that the nauplii of Pseudocalanus minutus grow more slowly when food concentrations are minimal. It was therefore hoped that the use of filtered lake water for these experiments resulted in the provision of a food supply similar to the conditions in the lake.

Observations on growth rates from instar analysis

Instar analysis of planktonic copepods in temperate waters by, for example SMYLY (1973), COMITA (1972), CARTER (1974) and GEORGE (1976) have shown the presence of clear growth cohorts following egg production in the Spring. In tropical waters, continuous reproduction results in a mixed population of instars throughout the year, but it was hoped that even with such minor fluctuations in population density, the estimation of growth rates would be practicable. However, it is clear from the results of instar analysis from site H1 samples in Figure 3.78 that cohorts of the type found in temperate populations are virtually non-existent. A guide to the accuracy of the laboratory experiments is, however, given by comparing the results of observed and expected instar compositions from the production calculations. Figure 3.78 indicates that the proportions of each instar found by calculating the expected composition and laboratory calculated growth rates are similar but overestimate the numbers of nauplii and adults. This suggests that mortality is highest in these two stages.

Results of net production rates calculated for Tropodiaptomus banforanus by the specific growth rate method.

Net production rates for T. banforanus at H1 and the Outer Buoy sites are shown in Table 3.14. The results indicate a mean rate of 0.00227 g/m^3 /day for the H1 site compared with 0.00103 g/m^3/day by the egg development time method. The mean production from the present method at the Outer Buoy site was 0.0195 g/m^3/day compared with 0.0480 g/m^3 /day by the earlier method. The two sets of results are therefore similar but, as neither is exact, they must both be considered.

Estimates of production rates in other lakes vary considerably. For example the mean annual production rate of Daphnia hyalina in a shallow eutrophic reservoir in Wales was shown by GEORGE and EDWARDS (1974) to be 0.57 g/m^3/day compared with SMYLY's (1973) estimate for Cyclops strenuus in a shallow eutrophic lake in England of 0.0017 g/m^3 /day. A comparison of the results from open water (H1) in Lake Turkana with lists of zooplankton production rates compiled from various sources by WETZEL (1975) and CUMMINS et al (1969) and WATERS (1977) shows that the net production of T. banforanus is relatively low. Most of these estimates are from temperate lakes and few comparable studies could be found for tropical lakes. BURGIS (1974) estimates the production rates of the most abundant zooplankton species for Lake George in Uganda, *Thermocyclops hyalinus*, as ranging from 0.0153-0.0287 g (dw)/m^3 /day, which is higher than that found for *T. banforanus* in the open water of Lake Turkana, but similar to the inshore (Outer Buoy) rate.

The question remains, however, as to which of the sites chosen for detailed analysis of production rates is most representative of Lake Turkana. Approximate calculations of net production in the different sectors using the egg development time and the less accurate determinations of clutch size and egg concentrations from routine zooplankton counts, shown in Table 3.15, indicate that the open water site H1 is most representative. This is supported from evidence of routine lakewide surveys of the concentrations and areal densities of *T. banforanus* described earlier (page 173) which show that concentrations rarely reached the levels found at the Outer Buoy site and were generally similar to those found at H1.

If therefore the results from H1 are taken as more representative of the whole lake, the annual production rate of *Tropodiaptomus banforanus* calculated from the egg development time was 11.737 g/m^2 and 25.86 g/m^2 by the specific growth rate method (≡11.727 - 25.28 tonnes (dry wt)/km^2).

The less accurate production rates shown in Table 3.15 calculated from the egg development time do, however, show a significant reduction in production from the north to the south of the lake, concomitant with a decrease in both primary production and densities of pelagic fishes.

SUMMARY

Spatial and temporal differences in the distribution and abundance of the zooplankton are described from vertical net hauls. The results show that small but significant changes in the zooplankton populations occurred on a seasonal basis associated mainly with the effects of inflowing water from the River Omo. Despite these changes the species composition, relative proportions and concentrations of zooplankton were extremely stable when compared with temperate lakes.

The crustacean species, particularly the calanoid copepod *Tropodiaptomus banforanus*, dominated the zooplankton in numbers and biomass. Rotifers were generally scarce and, although their numbers and species diversity increased near the Omo Delta, their contribution to total zooplankton biomass and production was unusually low. Many rotifer species are thought to be excluded from the lake by the relatively high salinity. In contrast to this, the protozoa species were found in relatively large numbers contributing on average 35% of the total number of zooplankters.

Little evidence for grazing by the common zooplankters on the dominant phytoplankton species *Microcystis* spp. and *Planctonema lauterbornii* was found but herbivorous cladocera and *Thermocyclops hyalinus* reduced in number when phytoplankton production was low. The dominant zooplankton *Tropodiaptomus banforanus* maintained relatively high densities in areas of low phytoplankton production and production and relied primarily on particulate detritus as a food source. *Mesocyclops leuckarti* was mainly carnivorous, particularly in the later stages of its development.

Predation by pelagic fish was found to be an important factor in the regulation of zooplankton populations. A comparison of production calculations with standing stocks in different areas shows that, although the production of *T. banforanus* was highest near the north end of the lake, standing stocks were either lower or similar to those found in the southern basin. Predation by the zooplanktivorous fish is thought to reduce standing stocks in the north and western areas to levels comparable with those found in the south.

The vertical distributions and diel migrations of the major zooplankton species are described and the adaptive values of these migrations are discussed. The unusual reversed vertical migrations of *Tropodiaptomus banforanus* is strongly correlated with the diel wind pattern. The downward movement of the adults and copepodites of this species at the onset of windy conditions is thought to reduce their exposure to lateral displacement by wind-generated surface currents. Despite this movement, a negative reaction to light, evident in most planktonic crustacea was still observed and may have been used as a more general reference point. *Mesocyclops leuckarti*, which preyed upon *T. banforanus* was also found to exhibit a reversed vertical migration but the other crustacea showed a normal diel migration descending during the day.

Production calculations for the dominant zooplankter *Tropodiaptomus banforanus* were carried out by two methods which gave similar results. The calculations indicate an annual production rate in the open water of between 11.7 and 25.3 tonnes dry wt/Km^2 and show a significant decline in production along the lake from north to south which is correlated with phytoplankton production and fish stocks.

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Hexarthridae		
Hexarthra jenkinae	Beauchamp	*
Keratella tropica	Apstein	
Crustacea		
Copepoda		
Calanoida		
Tropodiaptomus banforanus	Kiefer	*
Cyclopoida		
Mesocyclops leuckarti	Claus	*
Thermocyclops hyalinus	Rehberg	*
Thermocyclops emini	Mrâzek	
Ectocyclops hirsutus	Kiefer	
Microcyclops varicans	(Sars)	
Afrocyclops gibsoni	(Brady)	
Cladocera		
Sididae		
Diaphanosoma excisum	(Sars)	*
Daphnidae		
Hyalodaphnia barbata	Waltner	*
Ceriodaphnia rigaudi	Richard	*
Moina brachiata	(Jurine)	*
Moina micrura	Kurz	*

TABLE 3.2

Mean depths at which maximum concentrations of each species were found in the day under calm conditions in open water.

Species	Depth (m)
Vaginicola sp. nov. loricae	2.9
Vaginicola sp. nov. loricae with Vorticellids	3.4
Vaginicola sp. nov.	3.9
Felinia terminalis	4.1
Brachionus plicatilis	6.3
Raphidiophrys cf *pallida*	7.1
Tropodiaptomus banforanus	8.5
Hexarthra jenkinae	9.9
Mesocyclops leuckarti	11.3
Thermocyclops hyalinus	17.26
Moina brachiata	17.3
Ceriodaphnia rigaudi	17.7
Hyalodaphnia barbata	18.7
Diaphanosoma excisum	19.9

TABLE 3.3

Data matrix of variables used for the Principal Components Analysis on the depth distribution of *Tropodiaptomus banforanus*

Time	Sea	Light	W.temp.	M.numb.	Dist.X.	Scat	Wind	Depth	Site No
12.83	0	500	28.50	5.5	5.2	12.5	0	80	1
14.75	2	380	28.50	11.7	58.0	16.2	3	80	2
13.22	0	850	29.00	11.3	19.3	10.5	0	80	3
15.27	1	400	28.50	12.0	113.1	13.0	1	80	4
16.33	2	300	28.50	14.7	52.5	10.0	3.5	84	5
15.48	1	560	27.00	9.4	51.8	17.5	1	80	6
12.54	2	650	27.18	16.0	388.6	20.5	2	78	7
10.55	3	380	27.80	12.8	101.0	10.5	4	78	8
13.83	2	135	27.20	11.9	93.8	10.5	3	80	9
12.00	0	285	27.50	6.6	22.4	13.5	1	80	10
14.80	2	340	27.81	8.1	53.0	17.5	2	80	11
11.44	1	920	28.45	18.4	119.7	17.5	1	80	12
12.08	2	810	24.80	7.6	39.6	15.5	5	33	13
14.80	2	1400	26.52	9.44	124.58	18.5	4	55	14
14.86	0	480	27.32	10.99	68.38	11.5	0	42	15
09.53	3	110	26.20	21.62	135.13	13.5	4	38	16
12.25	2	1400	26.30	20.21	288.06	12.5	4	43	17
12.58	2	3600	26.82	14.6	383.0	27.5	5	54	18
15.25	3	2000	26.70	11.2	69.9	29.5	4	49	19
12.68	3	1200	27.20	13.5	72.7	14.0	2	35	20
15.66	3	54	26.60	22.9	84.4	9.5	3	40	21
13.54	2	2100	27.00	8.9	59.4	21.5	1	50	22
11.87	4	620	25.50	14.3	205.6	11.5	4	60	23
13.30	3	550	26.00	19.8	84.3	17.5	3	50	24
15.83	1	260	26.60	8.5	35.9	9.5	2	35	25
09.50	2	780	26.70	15.1	58.7	12.5	5	32	26
12.50	2	1100	27.00	10.8	116.1	15.5	4	55	27
11.50	3	1400	25.40	8.8	27.8	24.5	2	31	28
14.17	2	220	26.69	14.6	103.8	9.5	2	30	29
15.58	2	105	26.70	10.1	6.3	8.0	2	18	30
14.33	2	1300	27.00	10.9	59.2	10.5	2	82	31
13.50	3	460	26.58	7.9	23.4	9.5	4	21	32

Time	Sea	Light	W.temp.	M.numb.	Dist.X.	Scat	Wind	Depth	Site No
15.42	2	20	25.45	18.5	20.8	7.5	2	36	33
14.31	2	0.001	26.40	5.9	17.5	4.5	3	7	34
15.43	2	0.001	26.62	4.7	1.3	4.5	3	15.5	35
12.18	2	390	25.62	7.5	43.1	11.5	1	30	36
16.00	1	38	29.60	9.5	43.5	11.0	1	22	37
19.00	0	0.001	28.50	8.8	45.1	8.0	0	22	38
23.75	1	0	27.00	11.4	44.9	8.0	2	22	39
06.00	3	0.001	27.00	12.9	29.0	8.5	4	22	40
11.00	2	80	29.20	10.4	31.3	12.5	3	22	41
11.08	5	2500	24.50	18.36	133.58	26.5	8	50	42
13.08	4	4100	24.91	18.86	129.31	29.5	6	110	43
15.58	3	1800	24.68	17.81	53.81	24.0	5	52	44
12.66	4	4600	24.80	12.97	155.91	30.0	5	52	45

TABLE 3.4

Correlation matrix from variables used in the principal components analysis on the depth distribution of *Tropodiaptomus banforamus*

	T SCAT	S WD	L DP	WT	MN	DX
T	1.000000 -0.182470	-0.318433 -0.308164	-0.183591 -0.055979	0.136769	-0.194370	-0.161601
S	-0.318433 0.309833	1.000000 0.857151	0.229236 -0.071323	-0.613153	0.379660	0.338748
L	-0.183591 0.790274	0.229236 0.199232	1.000000 0.660069	-0.245840	0.239420	0.505211
WT	0.136769 -0.309099	-0.613153 -0.585700	-0.245840 0.110970	1.000000	-0.169960	-0.172149
MN	-0.194370 0.245523	0.379660 0.331271	0.239420 0.241613	-0.169960	1.000000	0.633832
DX	-0.161601 0.564919	0.338748 0.346563	0.505211 0.453289	-0.172149	0.633832	1.000000
SCAT	-0.182470 1.000000	0.309833 0.286595	0.790274 0.562839	-0.309099	0.245523	0.564919
WD	-0.308164 0.286959	0.857151 1.000000	0.199232 -0.050620	-0.585700	0.331271	0.346563
DP	-0.055979 0.562839	-0.071323 -0.050620	0.660069 1.000000	0.110970	0.241613	0.453289

TABLE 3.5

Component variance and proportions of the variance used for the components

Component Number	Component Variance	Proportion (%)	Total Proportion (%)
1	3.0092	42.99	42.99
2	1.9703	28.15	71.14
3	0.8951	12.79	83.92
4	0.4837	6.91	90.83
5	0.3096	4.42	95.25
6	0.1936	2.77	98.02
7	0.1386	1.98	100.00

TABLE 3.6

Component coefficients and correlations of variables with the components for PC1 and PC2

Variable	Component coefficient	Correlation coefficient
PC1		
Scat	0.4571	0.8353
Light	0.4463	0.8155
DX	0.4348	0.7946
Depth	0.3382	0.6182
MN	0.3277	0.5990
Sea	0.2979	0.5445
Time	-0.1904	-0.3480
WT	-0.2363	-0.4318
PC2		
Sea	0.5540	0.7110
MN	0.1365	0.1751
DX	-0.0607	-0.0780
Scat	-0.1584	-0.2033
Light	-0.2443	-0.3135
Time	-0.2499	-0.3206
Depth	-0.5069	-0.6505
WT	-0.5162	-0.6624

TABLE 3.7

Egg Development Times (hrs)

Species	Temp. °C								
	20	20.5	22	25	26	27.5	28	30	35
Tropodiaptomus banforanus	-	85.2	66.0	45.4	42.1	28.7	-	37.6	138
Mesocyclops leuckarti	81.8	-	66.5	-	51.5	-	42.8	-	-
Diaphanosoma excisum	-	-	61.3	42.0	-	-	-	-	-
Ceriodaphnia rigaudi	-	-	-	29.1	-	-	-	-	-
Thermocyclops hyalinus	-	-	-	-	-	-	-	30.1	-
Lake George (BURGIS, 1971)	59.2	-	-	39.3	-	-	-	28.6	-
Mesocyclops leuckarti									
Lake Chad (GRAS & SAINT JEAN, 1969)	-	-	56.0	38.0	-	-	-	25.0	-
Mesocyclops leuckarti									
Sweden (TAUBE, 1966)	52.0	-	-	42.0	-	-	-	-	-
Mesocyclops leuckarti									
Bodensee (EINSLE, 1968)	50.0	-	-	-	-	-	-	-	-

TABLE 3.8

Egg development times for Tropodiaptomus banforanus determined by the direct method

Temperature °C	Number observed	Mean development time (hrs)
25.0	17	44.7
26.0	30	42.7
30.0	29	38.4
35.0	All died	-

TABLE 3.9

Diel variations in egg production by pairs of *Tropodiaptomus banforanus*

Time of day (EAT)	Number of pairs which produced eggs	%
20.00 to 24.00	16	21.05
24.00 to 04.00	10	13.15
04.00 to 08.00	10	13.15
08.00 to 12.00	14	18.42
12.00 to 16.00	14	18.42
16.00 to 20.00	12	15.79

TABLE 3.10

Net production of *Tropodiaptomus banforanus* at Site H1

Date	No/1	Clutch size	No eggs/1	$D_{\hat{e}}$	B^1	T	P mg/1/day
11.1.73	9.55	2.6115	0.995	1.66	0.599	15.93	0.00582
19.1.73	6.37	2.00	0.730	1.60	0.456	13.97	0.004435
29.1.73	6.39	2.00	0.370	1.60	0.231	27.65	0.00224
12.2.73	4.26	2.612	0.341	1.55	0.202	19.32	0.00214
19.2.73	8.35	2.125	0.295	1.50	0.197	41.87	0.00191
27.2.73	8.91	3.130	2.279	1.50	1.520	5.87	0.01477
8.3.73	15.39	2.972	0.841	1.50	2.561	27.441	0.00544
6.4.73	9.98	1.891	0.717	1.50	0.478	20.87	0.00464

TABLE 3.11

Net production of *Tropodiaptomus banforanus* at Outer Buoy

Date	No/l	Clutch size	No eggs/l	D_e	B^1	T	P mg/l/day
22.3.74	137.24	3.74	36.27	1.29	28.11	4.88	0.485
28.3.74	58.01	3.85	12.465	1.25	9.97	5.82	0.14519
3.4.74	97.18	3.15	23.27	1.45	16.05	6.05	0.2838
21.4.74	94.50	2.70	10.31	1.45	7.11	13.29	0.1289
29.4.74	140.55	3.50	23.367	1.45	18.18	7.73	0.1612

TABLE 3.12

Sumbols used in description of the second method of estimating net production of *Tropodiaptomus banforanus*

N = Number per litre
D = Development time in days
W = Biomass
e = eggs
n = nauplii
CI = Copepodite stage I
to to
CV = Copepodite stage V
Ad = Adults (♂ and ♀)
E = Clutch size
P = Net production (mg/l/day)

TABLE 3.13

Mean development time in days for each stage of *Tropodiaptomus banforanus* determined from laboratory observations at 27°C and 29°C

Stage	27°C	29°C
E	1.4	1.5
N	2.3	5
CI	2	2
CII	2	2
CIII	4	4
CIV	6	6
CV	7	7

TABLE 3.14

Production rates for *Tropodiaptomus banforanus* calculated by Method 2

Date	mg(dw)/l/day	gm(dw)/l/day
(i) H1		
11.1 - 19.1.73	0.00241	0.1929
19.1 - 29.1.73	0.00114	0.0912
29.1 - 12.2.73	0.00209	0.1672
12.2 - 19.2.73	0.000994	0.0795
19.2 - 27.2.73	0.001496	0.1197
27.2 - 8.3.73	0.00251	0.2012
8.3 - 6.4.73	0.00525	0.420
	$\bar{x}$ = 0.00227	
(ii) Outer Buoy		
22.3 - 28.3.74	0.01626	0.1788
28.3 - 3.4.74	0.01537	0.1690
3.4 - 21.4.74	0.02625	0.2917
21.4 - 29.4.74	0.01997	0.2197
	$\bar{x}$ = 0.01953	

TABLE 3.15

Production rates of *Tropodiaptomus banforanus* in different sectors of the lake calculated by method 1

Sector and date	No/1	Clutch Size	Eggs/1	D_e	T (days)	P mg/ 1/d (dry wt.)
(i) March 1973:						
Omo	20.60	6.500	1.993	1.43	14.78	0.00203
North	51.32	3.915	13.051	1.40	5.51	0.0135
North Central	20.24	2.136	0.744	1.30	35.36	0.00083
South Central	20.79	2.158	5.308	1.48	5.79	0.00526
Turkwell	-	-	-	-	-	-
South	26.10	1.944	2.048	1.81	23.07	0.00166
(ii) June/July 1973:						
Omo	4.21	2.000	0.620	1.37	9.58	0.000644
North	28.32	2.335	2.752	1.30	13.37	0.00309
North Central	16.69	2.415	3.987	1.21	5.06	0.00484
South Central	33.28	2.078	2.197	1.34	20.29	0.002407
Turkwell	24.53	2.862	2.680	1.42	13.08	0.00275
South	16.93	2.379	2.333	1.83	13.27	0.00187

CHAPTER 4

A STUDY OF THE PRAWNS *Caridina nilotica (Roux)* and *Macrobrachium niloticum (Roux)* IN LAKE TURKANA

by

A.A.Q.R. McLeod

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4. A STUDY OF THE PRAWNS Caridina nilotica (Roux) AND Macrobrachium niloticum (Roux) IN LAKE TURKANA

A A Q R McLeod

INTRODUCTION

Two species of prawn, Macrobrachium niloticum (Roux) Palaemonidae and Cardinia nilotica (Roux) Atyidae have been identified from Lake Turkana. During the present sampling programme, both forms were at times abundant in the open water of the lake and were, in consequence, a potentially important source of food for predatory fish. The aims of the present study were to quantify the distribution of the two species, to investigate aspects of their biology, and relate these results to the behaviour of predator species.

Previous work on African freshwater prawns has been restricted chiefly to taxonomic problems and distributional records. The original examination of material from Lake Turkana collected by WORTHINGTON (1932) was carried out by GORDON (1933), who confirmed the presence of M. niloticum. Preliminary samples obtained during the present survey proved to contain both M. niloticum and C. nilotica (WILLIAMSON, 1974). Many African lakes include populations of two or more species of Caridea, but usually only one occurs regularly in the open water. Thus in Lake Chad M. niloticum was distributed ubiquitously throughout the lake basin, whereas Cardina africana was restricted to marginal vegetation (HOPSON, 1972). In Lake Victoria C. nilotica was the open water species and a similar situation was observed in Lake Mobutu (formerly Lake Albert) (GORDON, 1930). The coexistence of two pelagic Caridea in Lake Turkana appears to be unique in African lakes.

Ecological aspects of African freshwater prawns are poorly documented. HOPSON (1972), however, shows that in Lake Chad M. niloticum forms an important food resource for Lates niloticus, particularly in fish of 30-60 cm TL inhabiting the open water of the lake. HOLDEN (1967) reports that in Lake Mobutu (formerly Lake Albert) C. nilotica was the chief prey of Lates macrophthalmus which occupied a similar niche in the offshore waters to L. longispinis in Lake Turkana.

METHODS

Species descriptions published by GORDON (1933), BARNARD (1950) and BAILEY and CRICHTON (1971) were used to identify specimens.

A standard Marine Biological Association (UK) metre townet (see page 609) with an aperture size of 0.8 mm proved to be the most effective method for the capture of Caridea. This net retained all but the first zoeal stages of Caridina nilotica. Additional information on prawn distribution, particularly larger size classes of Macrobrachium niloticum, was obtained from tows made with the frame trawl (see page 603),Boris midwater trawl (see page 597) and from a parasitic bag attached to the cod-end of the bottom trawl (see page586). In each of these larger nets a stretched mesh size of 19 mm was employed.

Material was preserved in 5% formalin prior to examination in the laboratory. The wet weight of all samples was recorded. For larger catches, a volumetric subsampling technique was employed involving the use of a 30 ml dip prior to detailed examination. Replication proved that the subsampling method provided a satisfactory estimate of sample size ($t_s = 1.19$ for 9 degrees of freedom; $0.4 > P > 0.2$). Smaller subsamples were sorted into species and growth stages on a Bugarov tray, and the carapace length (CL) of each individual measured along the mid-dorsal line from the tip of the rostrum to the posterior margin of the carapace was also noted.

GROWTH

INTRODUCTION

Estimates of growth rates are necessary for the calculation of production rates based on standing stock measurements. Quantitative results derived from metre townet samples formed the basis of estimates of standing stock and growth rate obtained during the present survey, although in some cases valuable information was obtained from experimental work in the laboratory.

LENGTH-WEIGHT RELATIONSHIP

The study of length-weight relationships is based on the following data collected during September and October 1975:

(a) *Caridina nilotica* : 119 non-ovigerous prawns of 1-6 mm and 23 ovigerous females of 5-7 mm CL

(b) *Macrobrachium niloticum* : 154 non-ovigerous prawns of 1-12 mm and 34 ovigerous females of 7-11 mm CL

Individual lengths were measured to the nearest 0.1 mm and grouped into 1.0 mm size classes. Mean wet and dry weights for individuals in each size class were measured to the nearest 0.1 mg. Dry weights were obtained by drying to constant weight in a vacuum oven at 60°C. Mean class length plotted against mean class wet and dry weights are shown for the two species in Figures 4.1 and 4.2. The weighed geometric mean functional regressions (RICKER, 1973) show a linear relationship between $\log_{10}$ length and $\log_{10}$ weight for non-ovigerous prawns in both species (Table 4.1). The results indicate that in *C. nilotica* a prawn of 3.5 mm CL will undergo a weight loss of 84% on drying compared with 83% for a 4.5 mm individual of *M. niloticum*. The proportional loss decreases with increasing body length due to a higher proportion of exoskeleton in larger individuals.

In calculating the geometric mean functional regressions between CL and body weight, no allowance has been made for differing morphometry at different stages of the life cycle of the prawns. For the purposes of this paper, the overall relationship found between length and weight determined is adequate and there would be no significant increase in accuracy in producing the length-weight relationship for each growth stage.

In order to facilitate comparison of results presented in this paper with those of other species of Caridea, the relationship between CL and total length (TL) needs to be known (MAUCHLINE and FISHER, 1969). Total length is defined as the distance from the tip of the rostrum to the posterior margin of the extended telson. Results for 35 *C. nilotica* of between 1.4 and 6.8 mm CL, and 57 *M. niloticum* of between 1.1 and 16.8 mm CL are presented in Figure 4.3 and Table 4.2.

MATURITY STAGES

During the period June 1972 to November 1975, Caridea were recorded from a total of 394 metre townet samples from all areas of the lake, and the development stage and size frequency composition of the two species was recorded in each case.

The classification of maturity stages was modified from WILLIAMSON (1969):

Stage I : No pleopods present. Corresponds to zoeal stages I to IV
Stage II : Pleopods present, exopods on legs 1 to 4. Corresponds to zoeal stages V to VII
Stage III : Exopods on legs 1 to 4 not present. Corresponds to megalopa and juvenile stages
Stage IV : Adult
Stage V : Female bearing eggs, no embryonic eyes present in eggs
Stage VI : Female bearing eggs, embryonic eyes present

Length for stage data for the two species are summarised in Table 4.3. Stage I C. nilotica were small enough to escape through the meshes of the metre townet, but specimens caught in finer plankton nets show that they fell exclusively into the 0 mm size class. Stage II were found largely in the 1 mm length group, Stage III in the 2 mm, and Stage IV in length groups of 3 mm and above. Females became egg bearing at a minimum size of 4 mm and by a length of 6 mm CL, 50% of the population was ovigerous.

In M. niloticum, Stage I prawns were almost exclusively smaller than 2 mm CL, while Stage II and Stage III individuals fell principally into the 2 mm and 3 mm length groups respectively. A minimum length of 4 mm was observed in Stage IV individuals, and females became egg bearing at a length of 6 mm. By 9 mm CL, 50% of the M. niloticum population were ovigerous. The largest individual measured was a solitary specimen of 16.8 mm CL caught in the Boris midwater trawl.

HATCHING RATE

In both species, eggs are carried on the pleopods of females until hatching is complete. The eggs of C. nilotica are elliptical and measured 0.65 x 0.40 mm. Females between 5.2 and 6.2 mm CL carried between 11 and 15 eggs. The eggs of M. niloticum measured 1.05 x 0.90 mm and the number varied from 21 eggs in a female of 8.3 mm to 67 eggs in a female of 11.7 mm CL.

In order to investigate the hatching rate, a 70 litre tank was filled with freshly collected lake water and ovigerous prawns were introduced. The tank was not subjected to any temperature or light control, but was kept in a shaded room. Water temperatures fluctuated between a daytime maximum of 29 °C and a night-time minimum of 26.6 °C, which was comparable with that found in the open lake (see page 37).

Counts of the number of females in which hatching occurred were made at least once a day until no ovigerous females remained. The experiment was conducted once with 10 C. nilotica, and twice with 11 and 23 M. niloticum respectively. The results are presented in Figure 4.4, where the number of females with eggs, expressed as a percentage of the total, is plotted against time. Egg bearing individuals dying before hatching of their eggs have been ignored. There appears to be an initial latent or recovery period after capture, but trends indicate a hatching rate of 8 to 10 days for C. nilotica and a longer period of 17 to 23 days for M. niloticum. These results are comparable to those found by RASALAN et al (1968) for M. lanceifrons, a small tropical freshwater prawn of commercial potential.

ESTIMATES OF GROWTH

Estimates of growth rates for the Caridea in Lake Turkana have been made on observations of succession of maturity classes at sampling Station H1, situated in 80 m of water, 5 km north of Central Island. Oblique metre townet samples covering the whole water column were obtained at regular intervals between September 1972 and July 1974. Changes in the percentage of the maturity stages of the two species from sample to sample are shown in Figures 4.5 and 4.6. Although considerable fluctuations occurred from sample to sample in the proportions of the various developmental stages, no regular annual cycle is apparent in either species. The evidence suggests that increases in the proportion of young zoeal forms was foreshadowed, in both species, by an increase in the proportion of adults (and sometimes by berried females) a month previously. A high proportion of adults was not necessarily followed by an increase in the proportion of Stage I and II prawns, probably as a consequence of differing rates of adult mortality. The results indicate that peaks in the proportion of zoea tended to be followed three months later by a maxima in the juvenile portion of the population which led, after a further two months, to an increase in the relative numbers of adults. The evidence suggests that in Lake Turkana the two species mature in about five months, with Caridina nilotica possibly maturing slightly quicker than M. niloticum. The suggestion is reinforced by seasonal results derived from a lakewide analysis, discussed below.

Comparable results for other small tropical freshwater species of Caridea are few. Extrapolation of results obtained by RASALAN et al (1968) for M. lanceifrons, which matures at twice the size of M. niloticum, indicate that under laboratory conditions, this prawn matured in approximately six months.

LAKEWIDE DISTRIBUTION

Observations in the distribution of Caridea in Lake Turkana are based mainly on metre townet data covering the period September 1972 to November 1975. The 205 stations analysed were chiefly oblique hauls sampling the entire water column, but in a few cases stations were subdivided into several depth zones and the equivalent oblique haul was constructed from the combined data. Results are presented separately for the two species in Figures 8.59 and 8.60 which show the numbers per standard haul caught at each station for three periods of the year corresponding to the post-flood (November to May), pre-flood (June to July) and flood (August to October) seasons (see page 34). A standard haul is defined as having an equivalent surface area of 7.85 m^2 (see page 609) and the results shown in Figures 8.59 and 8.60 thus relate to areal densities. A large sample variance was evident at Station H1 where samples were obtained regularly; such a high variance was probably a prevalent feature throughout the lake, since population fluctuations were not of an annual nature (see below). The distribution maps have, as a consequence, not been discussed in absolute numbers, and regional and temporal differences have only been treated in relative terms.

Post-flood populations of both C. nilotica and M. niloticum extended throughout the lake with a tendency for densities to decrease in shallower water, except in regions of moderate shelter such as in the vicinity of the Kerio-Turkwell delta, Ferguson's Gulf and Koobi-Fora. In the pre-flood season, densities of both species tended to be low on the east side of the lake and high on the west. This trend was most marked in areas where the fetch of the prevailing south-easterly winds was greatest. During the flood season, densities of C. nilotica fell to almost zero in western parts of the Northern Sector affected by incoming flood water, and M. niloticum populations underwent a severe decline. Elsewhere prawn densities were maintained at levels similar to those observed during the other seasons, although few samples were obtained.

Two principal factors appear to influence the distribution of prawn populations throughout the lake, namely the influx of flood water and the wind. The incoming flood water caused a reduction in both transparency and conductivity (see page 50). The sediment plume resulting from the seasonal flood of the River Omo spread over most of the northern half of the lake and persisted well into the post-flood season. The effects were, however, greatest near the Omo delta where conductivities were considerably reduced. It seems likely that the population decline in the north of the lake resulted from the adverse effects of low conductivity and high sediment concentration on the physiology of the two species of Caridea. The former would impose a heavy osmoregulatory burden, and the latter a severe work load on the gill cleaning mechanisms. A narrow band of high population density might be expected on the southern fringes of the low conductivity area as a result of an avoidance reaction by the two species of prawn. Such high densities are in fact evident on the eastern side of the Northern Sector near Kakoi (Fig. 8.59b and 8.60b). Parallel investigations (see Chapter 3) show that the principal crustacean zooplankters undergo a similar population decline in areas of the lake most affected by inflowing flood water.

The prevailing south-easterly winds set up a circulation pattern which resulted in the building up of detritus near the west coast of the lake. High densities of both prawn and pelagic fish were observed in such coastal areas. The high detritus concentrations were undoubtedly enriched by the heavy concentrations of fish. Wind thus had an indirect effect on prawn distribution in that the population was controlled in part by the availability of food resources in the form of detritus. Analysis of gut contents of both species of Caridea showed the larger fraction to be of a very small particle size. Those items which could be identified were principally of crustacean and fish origin, and the proportion of algal matter was low. Crustacean remains could not be assigned to any one species and consisted only of setae and pieces of exoskeleton. The fish remains included two eye lenses, one of 0.45 mm diameter.

Analyses of lakewide distribution in the two species derived from oblique metre townet samples are presented in Figures 4.7 and 4.8.

The data have been grouped into three sectors, North, Central and South and eleven depth zones. Results are expressed both in terms of numbers and biomass of prawns per 100 m of surface area for each 1 mm length group. Weights were calculated from the length-weight relationships (see below). Where data were sparse, depth zones have been grouped together.

Both *C. nilotica* and *M. niloticum* were distributed in a similar manner in the clear water of the Southern Sector. Larval forms were present in all depth zones, with the smallest size class in both species showing no significant change in density in differing depths of water. The later zoeal stages of *M. niloticum*, in the 2 mm size attained a maximum mean areal density of 9.5 gm/100 m^2 in the 40-50m depth zone. Adult size, density, and areal biomass reached a peak in deep water, with individuals of greater than 7 mm CL attaining a mean density of 77.2 gm/100 m^2 in the 70-80 m zone. The highest areal densities of juvenile *C. nilotica*, 4.9 gm/100 m^2 , were observed in the 60-70 m depth zone, and adults of over 4 mm CL attained peak densities, biomass and mean size in the deepest areas, with a density of 2.0 gm/100 m^2 noted below the 80 metre contour. A similar trend was observed in the distribution of the two species in the Central Sector. The juvenile and smaller adult forms of *M. niloticum* of less than 4 mm CL were present at mean areal densities of up to 53.4 gm/100 m^2 in water of less than 40 metres deep. Such a high value did not occur in the case of *C. nilotica* where individuals of less than 3 mm CL reached a maximum mean areal density of 14.0 gm/100 m^2 in water of 0-40 m depth.

In contrast, prawns of all sizes were caught throughout the Northern Sector, with the exception of the 0-5 m depth zone. Both species demonstrated a tendency for the smaller length classes to occur more frequently in water of 20-40 m and larger sizes to occur more frequently in shallower water, a reversal of the situation observed elsewhere in the lake. Areal densities and biomass of zoeal and juvenile stages tended to be low compared with more southerly areas of the lake, but populations of adults showed no such decline and a value of 32.8 gm/100 m^2 for *M. niloticum* of greater than 7 mm CL was recorded in the 5-10 m zone of the Northern Sector.

Total mean areal biomass for all size classes of *C. nilotica* and *M. niloticum* in each 10 m depth zone for the three Sectors is shown in Figure 8.61. The values are principally a production of the distribution of the adult forms, except where the densities of smaller length groups were very high, as for example in the 10-30 m depth zone in the Central Sector. These areal densities have been used to derive lakewide biomass and production estimates discussed on page 615.

In the course of the shore survey (see page 559) *M. niloticum* was caught with a fine shore seine only at Ileret during October 1974 and at Todenyang, during August 1975. All specimens were adult, but no ovigerous females were present. *C. nilotica* was also virtually absent from inshore samples and was only occasionally caught by townet within Ferguson's Gulf. Zoeal stages of this species were, however, caught at night on the shore at Crater Bay, Central Island, where the coast shelves steeply into deep water. This occurrence was probably the result of combined vertical and inshore migration (see below).

The results prove that the Caridea of Lake Turkana were almost completely confined to the open waters of the lake. As mentioned previously, both *M. niloticum* and *C. nilotica* have been reported from a similar offshore habitat in other lakes. The lack of extensive marginal vegetation in Lake Turkana probably renders the environment unsuitable for shallow water demersal species such as Caridina africana which is widespread elsewhere in the soudanian region.

DIURNAL VERTICAL DISTRIBUTION PATTERNS

Preliminary samples from the surface layers of the open lake rarely contained adult Caridea but townets attached to bottom trawls caught larger individuals, suggesting that mean size of prawns increased with depth. Such effects are common in planktonic forms (MAUCHLINE, 1972). Frame trawl data (Fig. 8.31) provided a quantitative picture of the distribution of adult M. niloticum which were large enough to be retained by the net. The results confirm that during the daytime large specimens were principally confined to the demersal zone. Two series of horizontal tows made in the Longech area during August 1973 (Table 4.4 a and b) with the metre townet in Rig II (see page 610) showed that vertical zonation occurred in all size classes of both species of Caridea in Lake Turkana. Since an open net was used, samples were contaminated with specimens caught during the rapid transit of the net through shallower depths. It was evident that both the species of Caridea exhibited a decline in density within the scattering layer, which was nearer the surface in the more opaque water of Kerio-Turkwell delta origin (Table 4.4b) compared with the clearer water of the other site 2.8 km to the north (Table 4.4a). A further number of horizontal tows at various depths during February 1975, using an opening-closing metre townet Rig III (see page 610) were taken, and the results are summarised in Figure 4.9. In both species the tendency was for smaller more immature stages to occur above or just below the scattering layer, but rarely within it. Adult forms were generally distributed below the scattering layer with mature females in the deepest water, though adult C. nilotica were also observed above the scattering layer. All forms were generally absent from the top metre of the water column.

Horizontal tows within a chosen depth zone do not provide true estimates of the concentration within the zone, and a modified technique involving series of oblique metre townet tows was thus employed (see page 610). The results of a lakewide transect during February 1975 from Ferguson's Gulf to Allia Bay, using the improved method, are presented in Figure 8.45. Trends similar to those found in previous samples (Fig. 4.9) were observed. The scattering layer was generally situated at a depth of between 10 and 15 metres in inshore regions, descending to 20 metres in the deepest parts of the lake. Adult M. niloticum formed most of the biomass of Caridea except in the shallow water of Allia Bay where densities of zoeal and juvenile C. nilotica reached concentrations of 1.0 gm/100 m^3 . Measurements of echo integral (Fig. 8.46) show no correlation between concentration of Caridea expressed as mean biomass per unit volume and acoustic echo intensity per unit volume expressed as an integral voltage per unit volume. Integrals were highest within the scattering layer and just off the bottom, while Caridea concentrations were low within the scattering layer and maximal just under it.

A further series of vertically zoned oblique hauls were taken on a line of stations from approximately 2 km offshore into the mouth of Ferguson's Gulf (Table 4.5). This series of stations started at a point where the scattering layer impinged on the bottom and shows a trend of increasing numbers per unit volume, mean and maximum size, with increasing depth at any one station, and a marked reduction in concentration in shallower water falling to almost zero in the mouth of the gulf. The concentration of 2.2 gm/100 m^3 of adult Caridea within the scattering layer in the deepest station is probably due to the constraining effects of the bottom on vertical migration (see next section) and would appear to form an important source of food for predatory fish in this region.

VERTICAL DIEL MIGRATION

Although the frame trawl provided qualitative catches of only large M. niloticum, it was evident from preliminary studies (Fig. 8.35) that vertical migration occurred in this species, with adults restricted to the bottom four metres during the hours of daylight but tending to rise at night with the population dispersing over most of the water column. Two series of successive day and night stations using the opening-closing metre townet were run in the open lake near Longech, the first in July 1975 when the lake water was unaffected by the Omo flood water, the second in November 1975 after the peak of the flood season. During the first study the scattering layer was situated at a daytime depth of between 15 and 20 metres, but on the occasion of the second study, the layer had risen to a depth of between 5 and 10 metres as a result of reduced transparency.

The distributions of the two species of Caridea are summarised in Figures 4.10 and 4.11. The results for daytime samples were in general agreement with diurnal observations discussed above. Differences in areal densities are however evident with higher values during the November sample (Fig. 4.11). The significance of such differences is discussed below. No ovigerous female C. nilotica were caught in the July sample (Fig. 4.10) and the high density of C. nilotica in the night sample for that series probably results from patchiness in the distribution of prawns in the Longech area. Changes in the distributions with the onset of darkness are similar in both species. The youngest zoeal stages of M. niloticum (Stage I) exhibited a reversed vertical migration which was more marked in the November sample (Fig. 4.11). On this occasion, over 90% of the Stage I individuals occupied the 1 to 4 m depth zone during the hours of daylight, but with the onset of darkness virtually all these small prawn migrated downwards to concentrate near the bottom. During the July sampling period early zoeal stages of M. niloticum were established principally in the 5 to 10 metre depth zone during the hours of daylight. Aggregation in deeper water after dark was not so pronounced, and the young prawns tended to be distributed more uniformly with depth, with a notable exception of the 15-20 metre depth zone where none was recorded. Such sharp discontinuities in distribution in this and other stages are referred to below. As mentioned previously, Stage I C. nilotica were not sampled by the metre townet. Stage II M. niloticum was found principally above the scattering layer in daylight hours during both sampling periods, with only few individuals occurring below the lower limits of the scattering layer. Night-time distributions were considerably different, with the young prawns dispersed widely over the water column, although discontinuities indicate that certain depth layers were avoided. A similar pattern of behaviour occurred in Stage II C. nilotica. In both the July and November samples Stage III M. niloticum were distributed from below the scattering layer to the bottom during the hours of daylight, and dispersed upwards throughout the remainder of the water column after dark In the November sample over 40% of Stage III M. niloticum were found in the 1 to 5 metre depth zone during the night-time sample. In contrast, Stage III C. nilotica largely occupied a position above the scattering layer during daylight hours, but with the onset of darkness followed a similar dispersal pattern to Stage III M. niloticum, with concentrations increasing in deeper water. Maximum concentrations, however, remained in the 1 to 5 m depth zone.Stage IV to VII individuals of both species were found only towards the bottom of the water column during the daytime, but at night active vertical migration and dispersal occurred, with over 40% of the adults of both species occurring in the surface 10 metres.

Such changes in the distribution of the maturity stages of the two species of Caridea are similar to models suggested by CUSHING (1951), BAINBRIDGE (1961) and BODEN and KAMPA (1967) and reviewed by LONGHURST (1976). The ambient light intensity appears to be the factor controlling caridean behaviour in Lake Turkana with the daytime position in the water column a combination of water transparency and behaviour. The youngest stages occupied the top few metres of the water column, but avoided turbulence in the surface metre. Successively older life stages occupied positions further down, with adult and breeding individuals found only in the bottom few metres. Increased turbidity leading to a fall in light penetration resulted in an upward extension of the vertical range of all stages of both species. Such behaviour suggests that the prawns possessed a behavioural threshold to light intensity and would actively avoid higher levels of illumination. The acceptable levels of ambient light appear to have decreased with increasing age, thus giving rise to the observed distribution pattern with the zoea occupying a position at the top of the water column, and the adults at the bottom. Change in behaviour from a pelagic to demersal habit with the onset of maturity did not occur since adults were found in large numbers well clear of the bottom in the deeper parts of the lake. With the onset of darkness a response to the falling light intensity was an upward movement in an attempt to remain in the same light environment. Forms living in the top few metres quickly reached the surface and a passive sinking and dispersal phase then followed, except in the case of Stage I M. niloticum, a proportion of which appeared to undergo an active downward migration. Discontinuities in the overall trends of distribution of all stages of both species were noticeable both in day and night samples. A striking feature was the dearth of zoeal and juvenile prawns within the midwater scattering layer during daytime hauls. A similar absence is also evident at certain depths in night samples. Thus Stage I M. niloticum were absent from the 5-10 metre depth zone in the July sample. Such discontinuities were doubtless due to predation and avoidance of predators. The scattering layer was composed principally of Alestes ferox and Alestes minutus which fed continuously through the 24 hour period (see page 614) with prawns forming a high proportion of the prey during the latter half of the day. Demersal and deeper living pelagic fish such as Bagrus bayad and Lates longispinis were principally nocturnal feeders (see pages 1038 & 1323) rising in the water column with the onset of darkness to feed actively on the juvenile and adult stages of both species of Caridea. The results of the two diel studies for all maturity stages combined are summarised in Figures 8.47 and 8.48.

DISCUSSION

In both species of Caridea the distribution throughout the water column was a product of a diel behaviour pattern and water depth. Breeding individuals were found only in deep water and adults of both species were excluded from shallow water, except in the more turbid waters in the north of the lake. Diel migratory behaviour and dispersion by currents and lateral movement away from deep water breeding grounds would result in the wide and fairly uniform distribution of zoeal stages found in any one sector of the lake. Active upward nocturnal migration of juveniles and adults, combined with lateral dispersion, would tend to carry part of the population of larger prawns inshore, beyond the limits of their diurnal distribution. With the return of daylight such individuals would first move downwards in the shallower water and then offshore along the lake bed, down the light gradient, until the intensity was below the avoidance threshold. Results show that larger Caridea were confined chiefly to regions below the scattering layer, indicating that their light threshold was adapted to about this depth. High densities of Caridea observed in this particular zone (Figs. 4.7 and 4.8) probably resulted from such offshore movements during the post-dawn period of prawn in search of an acceptable light environment, leading to a concentration in the vicinity of the threshold. High densities of regularly replenished food would explain the presence of large numbers of predators of Caridea in the same locality, as recorded during the trawl surveys.

SEASONAL CHANGES IN POPULATION

The samples collected both at Station H1 and during the lakewide surveys were analysed for length frequency and frequency of maturity stages in both species of prawn. The results in this section have been presented on the basis of length frequency rather than maturity stages since more class intervals are available and trends are more easily recognisable. Length frequency data for oblique metre townet hauls at Station H1 have been combined on a monthly basis for both species of Caridea. The results (Fig. 4.12 a and b) are expressed as frequencies per standard haul. It is apparent that synchronous population changes at similar stages of maturity occurred in the two species, although absolute numbers differed. An increase in numbers of large adults was followed either by an increase in the frequency of the smaller size classes, or by a rapid decline of the entire population. Similar trends are evident in Figures 4.13 and 4.14 where all available data have been combined for each of the three main Sectors of the lake. Samples in the Northern and Southern Sectors were relatively infrequent. Although the magnitude of the catch differed from sector to sector, the relative proportions of each size class tended to be similar in months where results from two or more sectors were available.

It has been suggested earlier that maturation of Lake Turkana Caridea occurred in about five months, with C. nilotica maturing slightly more rapidly than M. niloticum, from consideration of the relative numbers of the various life stages of each species.

Trends in areal density of three size groups for each species within the Central Sector are shown on a $\log_{10}$ frequency plot (Figs. 4.15 and 4.16). The occasional samples taken after July 1974 are omitted. Although a high degree of reliance cannot be placed on individual points, the trends are significant. In most cases an increase in the density of mature individuals preceded a marked increase in the density of zoeal forms by approximately one month. This is consistent with the experimentally determined hatching rate. Where a zoeal population was persistent, the juvenile and immature adult population started to stabilize some three months later, but subsequent increases in the mature adult population were probably obscured by mortality. The time elapsing between a period of low zoeal density to a point where the population had recovered and a high zoeal density was observed was about five months for both C. nilotica and M. niloticum, which is consistent with the proposed generation length. Mortality probably varied from month to month and no regular seasonal pattern was apparent. Mean total areal densities of M. niloticum in the Central Sector (Fig. 4.17) showed four population maxima, in January, May and October 1973, and in March 1974, reaching a maximum frequency of 3160 individuals per standard haul in March 1974. Such regular maxima were not readily discernable in C. nilotica (Fig. 4.18) due to a greater overall population variation. A maximum frequency of 3790 individuals per standard haul was recorded in May 1975. Declines of total population noted in both species between March and April 1973, and between June and July 1974 were similar in nearly all size classes (Figs. 4.15 and 4.16). Densities of juvenile and immature M. niloticum fell less markedly than the corresponding stages of C. nilotica. In April 1973 densities of C. nilotica became too low to measure with confidence (Fig. 4.18) and this situation persisted until July 1973. Mortality in all size groups of C. nilotica seems to have been low before the August and November 1973 minima, while the population minima observed in M. niloticum at the same time were principally due to high mortality in the smaller size classes.

DISCUSSION

Since Lake Turkana presents a nearly constant physical and chemical environment, with the exception of the region to the south of the Omo delta, lakewide and simultaneous fluctuations in populations of prawn were certainly a result of increased mortality due to predation. Population densities for C. nilotica and M. niloticum indicated a resource limiting environment at extreme maximum densities and heavy predation at certain other times. Studies of feeding in offshore fish (see Chapters 9-12) show that many species, including Alestes ferox, Bagrus bayad, Schilbe uranoscopus, Synodontis schall and Lates longispinis, preyed extensively on prawns. The trophodynamic relationships between the prawns and their predators are a result of complex interactions between fish size and dietary preferences, prey and predator density, species composition and diel behaviour. On an energetic basis, there will be a density below which it becomes uneconomic for a predator to feed principally on a certain prey. Under such circumstances, a reduction in mortality due to predation would allow the prey population to recover, possibly reaching a stable maximum before the dietary preference of predator species again altered. Such a model could explain the observed fluctuations in prawn population in Lake Turkana. Density data have been used in conjunction with length-weight parameters to provide estimates of wet weight for the two species of prawn in kg/ha at population maxima and minima (Table 4.6). Although the two species contribute different proportions to the combined biomass, the total densities of Caridea at population minima are in the same order of magnitude, and always significantly lower than the widely ranging density maxima. A mean density of 0.25 kg/ha wet weight of prawn occurred at population minima, while densities rose to over 1000 kg/ha at maxima.

The data used in estimating lakewide biomass and production (see page 614 and Table 8.22) are combined from all oblique metre townet samples taken throughout the current survey, and as such are probably not significantly different from the average situation in the lake since samples were taken over a long period of time encompassing several population maxima and minima.

ECHO PHENOMENA ASSOCIATED WITH PRAWNS

INTRODUCTION

During the use of the high gain, high resolution Triton echo sounder on Lake Turkana (see page 626) it became apparent that certain types of echo were not attributable to trawlable fish. High echo integrals were at times recorded, generally in waters deeper than 30 metres, in areas where low trawl catches were obtained. Two echo types were recognised, the tall narrow 'plume', and the more continuous 'smoky trace' (Figs. 4.19 and 4.20).

METHODS AND RESULTS

It is thought that since the plumes were generally associated with narrow steep troughs (Figs. 4.19) from a few metres to tens of metres deep, that they were either a result of reverberation within the trough, or an echo return from objects within the water column. Inspection of traces lends support to the idea that they were caused by bubbles. Volcanic activity persists in the vicinity of the lake and gas vents have been observed on the main island, within the shallow water near the shore of Crater Bay, Central Island.

The smoky traces were investigated with the high resolution Alden recorder (Fig. 4.20) but, unlike the midwater scattering layer, could not be resolved into individual fish targets (Fig. 4.19). Sampling studies (see page 599) show that this layer was composed of fish only a few centimetres in length, and within the resolutions of the sounder employed. Smoky traces were common but not always present in the southern basin of the lake. The approximate limits of the traces during an acoustic fish survey in June 1975 are shown in Figure 4.21. Results of sampling a smoky trace with a bottom trawl during this cruise did not reveal any high fish concentration but an unusually large number of prawn were caught in the parasitic bag.

During August 1975, a detailed examination of smoky traces in the southern basin was undertaken from R V HALCYON. The extent and density of the traces were considerably less than those found during the earlier July cruise, the main concentration being limited to an area west of South Island in water of 50 to 60 metres depth. A total of four horizontal hauls with a combined frame trawl and plankton net, and five horizontal hauls with an opening-closing metre townet, were made. Half the frame trawl hauls and three of the metre townet hauls were taken in regions where the smoky trace was present, the remainder being control hauls. The frame trawl with a stretched mesh size of 19 mm retained only the largest prawns, and since all were capable of passing easily through the net, a high proportion undoubtedly escaped. The two hauls made in smoky traces caught up to nineteen times the weight of prawn taken in areas without the smoky trace, in identical haul times. The attached plankton net caught up to six times as much Caridea in areas with smoky trace compared to areas without smoky trace (Table 4.7). Quantitative hauls with the metre townet showed that the mean concentration of Caridea was up to twelve times higher in the regions with smoky traces (Table 4.8). Concentrations of the only other commonly caught small fish, Engraulicypris stellae, increased by a similar amount but concentrations within the smoky trace were only twice the minimum recorded for Caridea in regions clear of smoky traces, so clearly could not have been the cause of the observed phenomenon.

In all cases where the smoky trace was sampled Caridea formed a major part of the catch and were caught at higher densities than when the trace was absent. The proportion of catch obtained from the frame trawl contributed by Caridea fell in areas with no smoky trace, but remained high in six out of seven cases with the finer mesh nets. The relative proportions of Caridea and *E. stellae* remained fairly constant throughout the sampling area, with one exception which is discussed below. The sampling gear used in this investigation was capable of catching organisms between 0.5 mm and at least 600 mm in length. From the consistently high catches of Caridea obtained within the smoky traces it is evident that the principal cause of the strong echo returns was due to concentrations of *C. nilotica* and *M. niloticum* of at least 10 gm/100 m^3 .

In station 280-14 (Table 4.8) the smoky trace formed a dense patch situated within 10 metres of the bottom, and occupied 7% of the distance towed. The patch contributed over half the measured echo integral obtained during the haul. By applying the average density of Caridea from non-smoky trace stations 280-10 to 280-12, a catch of 540 prawn weighing 28 gm with a mean weight of 0.0050 gm is obtained for 93% of station 280-14. By subtraction it is estimated that the remaining 7% yielded a concentration of 2330 prawn per 100 m , weighing 156 gm with a mean weight of 0.0067 gm. The dense smoky traces are thus principally composed of adult Caridea since an individual *M. niloticum* weighting 0.0067 gm would be in the 6 mm length class. The presence of *C. nilotica* would depress this value of mean length. The dense patch sampled in station 280-14 had been detected a few minutes earlier when an integral of 50 mm was obtained over a volume of the same dimensions, indicating that prawn concentrations of 700 gm per 100 m^3 , and areal densities of 7000 gm per 100 m^2 , may at times occur in the deeper waters of Lake Turkana. These dense patches of small prawn would prove difficult to exploit since they are ephemeral, localised, and are principally found in more remote areas of the lake. The fine mesh trawls necessary for their capture would also retain large quantities of immature commercial fish, to the detriment of established fisheries.

The faint smoky trace recorded at metre townet station 280-12 (Table 4.8) was paralleled by a catch of 1.8 gm/100 m^3 of *E. stellae*, and a lower catch of Caridea, the only occasion on that survey when weight of *E. stellae* exceeded that of Caridea. It is probable that such densities of *E. stellae* represent a threshold at which a smoky trace can be generated. The smoky traces in the southern basin were principally demersal rising up to ten metres above the bottom.

During a cruise in August 1975 in the northern basin, a smoky trace was encountered that occupied a zone clear of the bottom, in 70 metres of water, west of Allia Bay. This trace was sampled with one horizontal metre townet haul (Table 4.8). The percentage composition and concentration of Caridea in this catch was low, the principal component being *E. stellae*. The catch density of 2.3 gm/100 m^3 of *E. stellae* was not high compared with the highest levels obtained for Caridea in the southern basin, but was 29% higher than the trace threshold level determined above. A higher echo level per unit of concentration could be expected due to the presence of an acoustically reflective swimbladder in *E. stellae*.

SUMMARY

Two species of prawn, Caridina nilotica and Macrobrachium niloticum occurred throughout Lake Turkana, forming an important food source for predatory fish. The investigation occupied the period June 1972 - November 1975 and most of the material was collected in a metre townet.

The length-weight and carapace length-total length relationship in both species was determined. Adult C. nilotica ranged from 3-8 mm (carapace length), and adult M. niloticum ranged from 4-12 mm (carapace length). Hatching rate of eggs in the two species was estimated to be ca 9 days in C. nilotica and ca 20 days in M. niloticum. Growth estimates show a general period of ca 5 months.

Distribution of both species was similar with areal density greatly influenced by conductivity and wind; the main concentration occurred on the west side of the lake. Larger individuals tended to be confined to deeper water but a great proportion of all maturity stages were fully pelagic, principally occupying the open water. During the hours of daylight all maturity stages were generally absent from the scattering layer, with juveniles concentrating above the scattering layer, adolescents and adults occurring at progressively greater depths below the scattering layer. Diel vertical migration took place in all maturity stages of both species. Variation in areal density of both species was shown to be cyclic, but was not correlated with the seasons.

High densities of prawns were shown to be the cause of diffuse deepwater traces registered on a high resolution echo-sounder.

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TABLE 4.1

Length-weight relationship on a geometric mean functional regression of non-ovigerous *C. nilotica* and *M. niloticum* where w = weight in grams, CL = carapace length in mm, u and v = constants, r = correlation coefficient.

G M regression:- $\mathrm{Log}_{10}w = \mathrm{Log}_{10}u + v\,\mathrm{Log}_{10}CL$

Species	Wet			Dry			Number of individuals
	u	v	r	u	v	r	
C. nilotica	5.26×10^{-4}	2.39	0.995	7.63×10^{-5}	2.51	0.997	119
M. niloticum	2.91×10^{-4}	2.07	0.993	4.12×10^{-5}	2.19	0.994	154

TABLE 4.2

Geometric mean functional regression between carapace length and total length for *C. nilotica* and *M. niloticum*. Where CL = carapace length in mm, TL = total length in mm, u and v = constants, and r = correlation coefficient.

G M regression:- $TL = u + vCL$

Species	u	v	r	Number of individuals
C. nilotica	1.51	2.13	0.98	35
M. niloticum	2.75	2.26	0.99	57

Table 4.3

Changes in the maturity of (a) *C. nilotica* and (b) *M. niloticum* with size, showing the percentage at various stages of maturity in 1 mm length classes for all measured specimens caught during routine metre townet samples between June 1972 and November 1975.

(a) *C. nilotica*

Length group (CL in mm)	Number of prawn	Stage I	Stage II	Stage III	Stage IV	Stage V-VI
1	8581	-	69	30	1	-
2	4084	-	+	98	2	-
3	1146	-	-	35	65	-
4	481	-	-	-	100	+
5	256	-	-	-	84	16
6	91	-	-	-	29	71
7	24	-	-	-	17	83
8	3	-	-	-	33	67
TOTAL	14666					

(b) *M. niloticum*

Length group (CL in mm)	Number of prawn	Stage I	Stage II	Stage III	Stage IV	Stage V-VI
0	4	100	-	-	-	-
1	2260	96	4	-	-	-
2	3164	+	97	2	+	-
3	1692	-	-	93	6	-
4	1209	-	-	6	95	-
5	1137	-	-	-	100	-
6	924	-	-	-	100	+
7	348	-	-	-	99	1
8	186	-	-	-	65	35
9	88	-	-	-	48	52
10	17	-	-	-	41	59
11	5	-	-	-	40	60
TOTAL	11034					

TABLE 4.4

Showing the occurrence of Caridea in a series of horizontal metre townet samples made at various depths at two stations 2.8km apart, off Longech Spit, during August 1973. Limnologised conditions at the two stations differed considerably. The samples were obtained at a towing speed of 5.4km/hr for a tow duration of 5 minutes at the sample depth.

(a) Station 122-1 14.45 to 16.07 hrs in 28 metres of water, 4.3km NNE of tip of Longech Spit. Water clear and green in colour. Scattering layer at 15 to 18m.

Depth of net (m)	C. nilotica			M. niloticum		
	Number per tow	Mean length (mm)	Maximum class length (mm)	Number per tow	Mean length (mm)	Maximum class length (mm)
0	0	-	--	0	-	-
6	321	2.0	2	693	2.1	2
8	112	2.0	2	226	1.9	2
12	No data			No data		
16	32	1.8	3	33	1.7	2
18	18	2.0	3	1	1.5	1
20	17	2.2	3	20	2.1	2
23	451	2.9	5	401	3.6	6

(b) Station 122-2 16.50 to 18.20 hrs in 19 metres of water, 1.8km NE of tip of Longech Spit. Water brown with sediment from Turkwell and Kerio Rivers. Scattering layer from surface to 9m.

Depth of net (m)	C. nilotica			M. niloticum		
	Number per tow	Mean length (mm)	Maximum class length (mm)	Number per tow	Mean length (m)	Maximum class length (mm)
2.5	112	2.2	3	7	2.2	2
4	9	2.5	3	4	2.8	3
6	-	-	-	-	-	-
7	6	2.2	2	-	-	-
8	90	2.2	2	112	3.4	4
10	98	3.2	5	210	4.4	8
12	102	3.9	5	102	4.4	7
14	105	4.0	5	97	4.5	6

TABLE 4.5

Concentration of C. nilotica and M. niloticum at four metre townet stations in the locality of Ferguson's Gulf in August 1975. Results are expressed as mean catch per $100m^3$

Depth zone (m)	*C. nilotica*				*M. niloticum*			
	Number	Biomass (gm)	Mean length (mm)	Max. class length(mm)	Number	Biomass (gm)	Mean length (mm)	Max. class length(mm)
Station 275-1	Scattering layer 10 to 16 metres			1.4 km NNE tip of Longech Spit				Depth 16 m
0- 1	-	-	-	-	-	-	-	-
1- 5	2.7	+	1.5	1	0.5	+	1.5	1
5-10	18.8	0.03	2.2	2	64.9	0.28	2.4	2
10-Bottom	471.0	1.54	3.2	4	801.0	0.68	2.5	3
Station 275-2	Inshore from scattering layer			2.3 km NNW tip of Longech Spit				Depth 10 m
0- 1	2.0	0.01	2.7	3	-	-	-	-
1- 5	0.7	+	3.0	3	0.5	+	1.5	1
5-Bottom	4.2	0.01	2.4	3	4.5	0.02	2.5	2
Station 275-3				0.5 km N of entrance to Ferguson's Gulf				Depth 5.5 m
0	-	-	-	-	-	-	-	-
1-Bottom		No data				No data		
Station 275-4				0.5 km S of entrance to Ferguson's Gulf				Depth 3 m
0	-	-	-	-	-	-	-	-
1-Bottom	-	-	-	-	0.9	+	2.5	2

TABLE 4.6

Maximum and minimum areal densities in kg/ha for C. nilotica and M. niloticum in the Central Sector of Lake Turkana between October 1972 and May 1974.

Date	C. nilotica	M. niloticum	Total Caridea
	Maximum areal density in kg/ha		
January 1973	3.44	5.14	8.58
May 1973	0.13	5.37	5.38
October 1973	9.71	4.87	5.84
March 1974	72.6	1068.4	1141.0
May 1974	104.1	473.0	577.1
Mean March - May 1974	88.4	770.7	859.1
	Minimum areal density in kg/ha		
October 1972	1.48	1.63	3.11
April 1973	0.00	3.37	3.37
August 1973	0.35	1.42	1.77
November 1973	0.28	1.10	1.38

TABLE 4.7

TABLE 4.7

Results of four ten minute horizontal tows made in the southern basin of Lake Turkana during August 1975 with a 2.9 x 2.9m frame trawl and an attached 23.6 mesh per cm 48cm diameter townet.

					Principal component of townet catch			Frame trawl catch *Macrobrachium niloticum*			*Engraulicypris stellae*			Remainder			
Station number	Depth bottom (m)	Depth tow (m)	Echo integral in mm during tow in a 3m gate at depth of tow	Description of smoky trace and depth range	Species	Weight (gm)	% total weight	Number	Weight (gm)	% total weight	Number	Weight	% total weight	Species	Number	Weight	% total weight
280-6	54	50-53	25	Moderate 51-53m	Caridea	40	70	412	56	80	19	3	4	A. *ferox*) A. *minutus*) B. *turkanae*)	15	11	16
280-7	56	52-55	26	Moderate 52-55m	Caridea	50	70	1110	126	79	90	17	11	A. *ferox*) B. *turkanae*)	16	17	10
280-8	62	58-61	4	Nil	Caridea	10	80	70	10	11	2	1	1	A. *ferox*) B. *turkanae*) C. *auratus*) L. *longispinis*) H. *macconneli*)	13	81	88
280-9	63	59-62	4	Nil	Caridea	8	80	41	7	6	0	-	-	B. *turkanae*) S. *schall*) H. *macconneli*)	5	98.8	94

TABLE 4.8

Results of four horizontal tows made with an opening-closing metre townet in the southern basin, and one tow made in the northern basin of Lake Turkana, in August 1975.

						M. niloticum and *C. nilotica*				*Engraulicypris stellae*			Remainder
Station number-Location	Depth bottom (m)	Depth tow (m)	Echo integral in mm during tow in a 3m gate at depth of tow	Description of smoky trace and depth range	Volume of tow (m^3)	Principal component	Number per $100m^3$	Weight gm/ 100^3	% total weight	Number per $100m^3$	Weight gm/ $100m^3$	% total weight	% total weight
Southern basin													
280-10	63	62	-	Nil	1075	Adults	45	2.7	93	2	0.2	7	1
280-11	64	63	-	Nil	778	Adults	25	1.2	80	3	0.3	20	1
280-12	57	55	-	Faint, 53-57m	1338	Adults	26	1.1	38	16	1.8	62	1
280-13	56	53	5.5	Slight & patchy 52-56m	979	Adults	305	13.6	85	17	2.4	15	1
280-14	57	54	11 in patch 21 overall	One dense patch 47-57m	1819	Adults	185	11.92	86	14	1.9	14	1
Northern basin													
281-19	70	45	-	Moderate 35-55m	728	Adults	15	0.4	15	26	2.3	85	1

CHAPTER 5

THE FISHES OF LAKE TURKANA

by

A. J. Hopson and J. Hopson

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A J and J Hopson

INTRODUCTION

This chapter provides an introduction to the ichthyofauna of Lake Turkana as a preliminary to detailed studies of fish biology and assessments of commercial fish stocks which follow. The objectives are twofold, firstly to afford an inventory of the species of fish occurring in the area together with accompanying notes on their ecology, distribution and economic importance and secondly, to provide the means for accurate identification of each fish. The area under consideration includes the whole of the main lake together with the deltas of the Rivers Omo, Kerio and Turkwell. For most species the supplementary notes summarise detailed information which appears in later sections but in a few cases, where the lack of data has precluded lengthy analysis (e.g. *Heterotis niloticus*) it was found convenient to include all relevant facts in the present chapter. Morphological details are based wherever possible on material collected from Lake Turkana during the present survey. In a number of species larval, post-larval and juvenile stages were obtained and for ease of reference descriptions of these have been grouped together at the end of the main systematic section.

HISTORICAL BACKGROUND

The earliest collections of fish from the Turkana basin were made by the American traveller Dr Donaldson Smith during two visits to the north east corner of Lake Turkana, the first in 1895 and the second in 1900. More comprehensive collections from the River Omo and from the north end of the lake were carried out in 1908 by Messrs Zaphiro and McMillan. Details of the material obtained during these pioneer visits appear in BOULENGER (1909 and 1915).

No further extensive collections were made until 1930-31 when the Cambridge University Expedition carried out a detailed survey of the central area of the lake from a base at Ferguson's Gulf. The expeditionnoted 17 previously unrecorded species of fish, raising the total number known to occur within the lake to 35. The additions included 8 new species or subspecies (WORTHINGTON, 1932; TREWAVAS, 1933; WORTHINGTON and RICARDO, 1936). This expedition was soon followed by the 1932-33 Mission Scientifique de l'Omo which obtained fish from the River Omo and its detla. The collection was studied by PELLEGRIN (1935) and contained 3 further species, including one new taxon.

More than twenty years elapsed before the ichthyofauna was again investigated. HAMBLYN (1960) visited the Ferguson's Gulf area in 1960 and gives details of gillnet catches in the area. During a subsequent visit he collected fish in the Loiengalani area and lists a total of 10 species (HAMBLYN, 1962). MANN (1964) fished extensively in the vicinity of Ferguson's Gulf and provides detailed information on species caught together with a synopsis of previous records from the lake.

During the present investigations a total of 12 species, including 5 new endemic forms, were added to the list of Lake Turkana fish. The total ichthyofauna now stands at 48 species, 10 of which are endemic. This takes into account previous misidentifications and a recent revision of large Barbus (BANISTER, 1973) which has led to the synonymising of several previously recorded species.

ZOOGEOGRAPHY

Vast areas south of the Sahara from the Gambia, through the Senegal, Niger, Volta, Chad and Nile basins share a similar fish fauna. These areas form a single icthyogeographical region which BEADLE (1974) has termed the 'soudanian' region to replace the earlier and more ambiguous term 'nilotic'. The soudanian fauna consits of approximately 40-50 species of fish including such forms as Alestes baremose, Citharinus citharus, Bagrus bayad, Lates niloticus and Sarotherodon niloticus. The exact number is difficult to estimate since certain forms with only a limited distribution are replaced in other parts of the region with allopatric species which might, on closer inspection, prove to be more closely related. Most large river basins within the region also contain numerous species of localised or endemic fish but these are often relatively uncommon or restricted to a specialised habitat. Soudanian fish by contrast are usually the dominant species in terms of numbers or biomass and tend to form the basis of the major fisheries throughout the region.

The geological events leading to the establishment of Lake Turkana in its present form are discussed in Chapter 1 (see page 3). There is clear evidence to prove that the lake was connected to the Nile system by an outflowing river as recently as 7000 years ago. With such a recent connection it is not surprising to find that of 48 species occurring in the environs of the contemporary lake, 30 are characteristic soudanian species with ranges extending from the Nile to West Africa. Lake Turkana clearly forms an integral part of the soudanian icthyogeographical region. Nearly all the remaining 18 fish occur also in the Nile or are endemic species whose phyletic origins are obviously soudanian or nilotic.

ENDEMIC SPECIES

It has been a matter of much speculation as to why speciation, particularly among cichlid fish, should be such a feature of certain major East African lakes, such as Victoria, Tanganyika and Malawi, but virtually absent in others. The low level of endemism in Lake Turkana and Lake Mobutu (formerly Lake Albert) has been noted by various authors including LOWE-McCONNELL (1969), FRYER and ILES (1972) and GREENWOOD (1974). Recent amendments to the fauna list of Lake Turkana have not markedly changed the situation, and revised proportions of endemic cichlid and non-cichlid fish in the two lakes are shown in Table 5.1.

This situation may result from the way in which the various lakes were originally colonised. Lakes which developed in comparative isolation from the major river systems, such as Lakes Victoria, Malawi and Tanganyika, would be populated initially by a scant fauna derived from minor rivers, pools, springs etc. The species involved would tend to be unspecialised forms with generalised feeding habits. With the advent of lacustrine conditions the complexity of the environment would increase considerably to provide many additional ecological niches. Such circumstances would provide the necessary stimuli for speciation to proceed. Subsequent changes in drainage pattern would probably occur, resulting from time to time in the augmentation of the lacustrine fauna by fresh colonisers. It seems likely, however, that the predominantly endemic character of the fauna would be established during the early period of colonisation.

Conditions were probably different in the case of Lakes Turkana and Mobutu which have been in direct contact with the River Nile for extensive periods of their history. The fauna of the River Nile, as mentioned previously, is basically soudanian in character. The ancient origins of this fauna, which can be traced back to early Pliocene times, indicate a high degree of stability. It seems likely that when the contemporary faunas of the lakes were originally established, connections with the Nile were open. This would result in colonisation of the new lake basins by an already well differentiated fauna. Environmental conditions suitable for riverine species would already exist in inshore areas of the lake and the surface waters offshore. Under these circumstances one would not expect a marked tendency for speciation.

Riverine species are, however, less well fitted for life either in the midwater layers of a large lake or on the bottom in deeper water offshore, and it is interesting that in Lake Turkana endemism is most apparent in these two habitats. Three endemic species, *Alestes ferox*, *A. minutus* and *Lates longispinis* are dominant in the midwater community which extends throughout the open waters of the lake. A fourth endemic species, *Engraulicypris stellae*, occurs abundantly in the same habitat but also ranges inshore. *Alestes ferox* and *A. minutus* are almost certainly sympatric species which have evolved from *A. nurse*, a fish now restricted to the littoral region of the lake. *Lates longispinis* probably has a similar phyletic relationship with *L. niloticus*.

Three of the four species forming the demersal community in the deeper waters of the lake are also endemic. Of the endemic forms *Haplochromis turkanae* and *Barbus turkanaae* show no particular specialisation but *Haplochromis macconneli* has a hypertrophied latero-sensory system which is clearly an adaptation to life in deep water.

FISH COMMUNITIES

The distribution of individual species of fish in Lake Turkana will be considered at length in succeeding chapters but it is appropriate at this point to make certain generalisations concerning the pattern of occurrence. Of the 48 species recorded from the vicinity of Lake Turkana, 36 occur regularly within the actual lake. The remaining 12 species are restricted to the area of the Omo detla.

In the main lake a few species, for example *Engraulicypris stella*, *Barbus bynni*, *Synodontis schall* and *Lates niloticus* were found to occur commonly over a wide range of habitats both inshore and offshore. Most species, however, had a relatively narrow range of tolerance and tended to be restricted to a particular type of habitat. Such preferences were usually shared by a number of species of fish which associate together in what, for the purposes of the present study, has been termed a community. It will be appreciated that in each community, fish form only part of an ecosystem which includes a variety of organisms at all trophic levels. The degree to which members of a community interact with one another varies considerably. During the hours of darkness the boundaries between the various communities tended to break down and a general movement of fish towards the surface and inshore was evident.

Four major communities of fish have been recognised in the main lake (Fig. 5.1):

(a) Littoral

(b) Inshore demersal

(c) Offshore demersal

(d) Pelagic

Their boundaries shift seasonally and are determined chiefly by the light climate. A reduction in underwater illumination during the turbid flood season stimulates fish living in the subsurface layers to move nearer the surface and closer inshore. Communities (a) and (b) are subdivisible on the basis of substrate.

(a) *Littoral community*: restricted to an inshore belt between the lake margin and the 4 m contour. *Sarotherodon niloticus* and *Clarias lazera* occur throughout; *Barilius niloticus* and *Tilapia zillii* prefer rocky or stony shores; *Sarotherodon galilaeus*, *Alestes nurse*, *Micralestes acutidens* and *Chelaethips bibie* prefer soft substrates and *Haplochromis rudolfianus* and *Aplocheilichthys rudolfianus* favour submerged and emergent macrophytes.

(b) *Inshore demersal community*: bottom-living fish restricted to inshore areas of the lake between the 4 m contour and a depth of 10-15 m. Characteristic species on soft substrates are *Labeo horie*, *Citharinus citharus* and *Distichodus niloticus*. Relatively little data are available for rocky substrates situated at equivalent depths but *Bagrus docmac* probably occurs regularly in such areas.

(c) *Offshore demersal community*: ranges throughout the deeper waters of the lake in a narrow layer rising 3-4 m above the lake bed. The inshore limits vary from 8 to 20 m depending on the season. Characteristic species are *Bagrus bayad*, *Haplochromis macconneli* and *Barbus turkanae*.

(d) *Pelagic community*: spread over the entire water column from the upper limits of the demersal communities to the surface, and encompassing both inshore and offshore regions of the lake. Pelagic fish tend to be stratified by depth and three distinct faunal layers have been recognised:

(i) The *superficial layer*: extending downwards from the surface to the midwater scattering layer. *Hydrocynus forskalii* and *Alestes baremose* are the dominant species with distributions ranging from the fringe of the littoral zone into mid-lake. Post-larval *Engraulicypris stellae* and early stages of the prawns *Macrobrachium niloticum* and *Caridina nilotica* are also characteristic of the superficial layer.

(ii) The *midwater scattering layer*: consisting of pelagic fish which concentrate in a discrete zone several metres in vertical extent, resulting in a characteristic trace on echo records. The position of the scattering layer varies with transparency from a depth of less than 5 m in the turbid waters of the Northern Sector during the flood season to more than 30 m in the southern basin. *Alestes minutus* and *A.ferox* are the principal species involed, together with smaller numbers of the predators *Lates longispinis* and *Schilbe uranoscopus*.

(iii) The *deep pelagic layer*: situated between the midwater scattering layer and the demersal zone, extending over a depth range of up to 60 m in the deeper sections of the lake. Larger fish are scarce in this layer but adult *Engraulicypris stellae* tend to be widely dispersed throughout. Adult prawns also concentrate in the deep pelagic layer.

SPAWNING SITES

The nature of spawning movements varies considerably from species to species. In some fish, ripe individuals undergo long distance migrations which carry them from all parts of the lake to spawning grounds situated in the River Omo. At the other extreme, cichlids often move only within localised inshore areas of the lake to sites where conditions are suitable for nest construction. The more important fish of Lake Turkana are grouped below according to location of their spawning sites:

(a) Spawning only in the River Omo:

Alestes baremose

A. dentex

Citharinus citharus

Distichodus niloticus

Barbus bynni

(b) Spawning in both the River Omo and the delta of the River Kerio:

Schilbe uranoscopus

(c) Spawning within the mouths of both the major rivers and ephemeral rivers during periods of spate:

Alestes nurse

Labeo horie

Clarias lazera

Synodontis schall

(d) Spawning in the littoral region of the lake:

Barilius niloticus

Aplocheilichthys rudolfianus

Tilapia zillii

Sarotherodon niloticus

S. galilaeus

Haplochromis rudolfianus

(e) Spawning away from the shore in the open lake:

Alestes ferox
A. minutus
Engraulicypris stellae
Bagrus bayad
Lates longispinis
L. niloticus
Haplochromis macconneli

Populations of *Hydrocynus forskalii* appear to be divided between individuals which spawn within the lake and those which undergo a spawning migration into the River Omo.

FOOD

The feeding habits of the principal species of fish are considered in detail in subsequent chapters. Figure 5.2 provides a synopsis of the results. Most food resources are well utilised with one important exception; *Microcystis aeruginosa*, the dominant alga in the open waters of the lake was not grazed on regularly by either fish or planktonic crustacea. However, during periods when zooplankton populations were seasonally low in the Northern Sector, the characin *Micralestes acutidens* switched to algal food and successfully assimilated *Microcystis*.

TAXONOMIC METHODS

The systematic descriptions of fish which follow are based to a great extent on counts and measurements. The nature and extent of each of the routine measurements carried out is indicated in Figure 5.3. Standard length (SL) has been used for all descriptive work; this is the length of the body from the tip of the snout to the base of the caudal fin where it joins the body. Care should be taken in making this measurement since scales usually overlap the fin base. The length of snout was measured diagonally from the anterior margin of the eye orbit to the tip of the snout. The bony interorbital width was always used. Simple or spinous fin rays were counted separately from branched rays and their numbers indicated by Roman numerals followed by the branched fin ray count in Arabic numerals. In most species the last branched dorsal and anal fin rays are double but were counted as a single ray. In the systematic descriptions the range of fin ray or lateral line scale counts is often followed by the modal number (M). The frequency (f) of a particular count is sometimes also shown.

In most cases the systematic descriptions which follow are based on material collected during the present survey, and the number and size range of the fish examined is indicated. Where no such indication of number and range appear, the descriptions are based on information from BOULENGER (1909, 1911 and 1916).

PIGMENTATION

GREENWOOD (1974) noted that the ovary wall and peritoneum of *Haplochromis rudolfianus* from the Central Sector of Lake Turkana were unusually heavily pigmented with melanin. He considered that the phenomenon was probably correlated with the intense sunlight to which shallow water fish would be subjected in the area. Abnormally heavy pigmentation has been noted in other species of fish living in shallow areas of Lake Turkana, particularly in the southern basin where the water is clearest. In Loiengalani Bay and off South Island entirely black specimens of both Synodontis schall and Bagrus docmac were seen and both Sarotherodon niloticus and Haplochromis rudolfianus were considerably more darkly pigmented than was the case in more northerly areas.

SYSTEMATIC DESCRIPTIONS

Family Polypteridae

Genus Polypterus Geoffroy Saint-Hilaire, 1802

Polypterus and a little known West African genus Calamoichthys (a very elongated fish lacking pelvic fins) are the sole representatives of a group of fish with obscure though undoubtedly archaic origins. They are readily recognised by the form of the dorsal fin which is subdivided into a number of separate finlets, each consisting of a spine, bifid at the tip with a sail-like membrane supported by rays extending posteriorly. The body is long and cylindrical, clad with shiny rhombic scales arranged in oblique rows. The pectoral fins are borne on pronounced peduncles covered with scales. Unusual internal features include the modification of the swimbladder to form a lung-like breathing organ. Two species of Polypterus have been identified from Lake Turkana.

Polypterus senegalus Cuvier, 1829

(Fig. 5.4)

Turkana name: nagiri

This species was first collected from Lake Turkana by Zaphiro and McMillan in 1908 (BOULENGER, 1909). Subsequent material was obtained by the 1932-33 Mission Scientifique de l'Omo (PELLEGRIN, 1935). During the present survey the species was caught in small numbers at the extreme north of the lake.

Description: based on 14 fish ranging from 20.1 - 37.5 cm SL
Body cylindrical, interorbital space convex. In all but one fish the tip of the pectoral fin did not overlap the vertical to the first finlet. Number of dorsal finlets 8-10 (M=9), lateral line scales 56-60 (M=57), scales round body 34-39 (M=35), scales between occiput and first finlet 16-19 (M=18).

Colouration: uniform brown above, lighter on the ventral surface, free from mottling.

Food: Chiefly insectivorous but also preys on small fish

Distribution: restricted to the extreme north of Lake Turkana close to the Omo delta. Not recorded from offshore stations and probably entirely littoral in distribution occurring chiefly in well vegetated situations. Most specimens were caught in shore seines.

Widely distributed throughout the soudanian region of Africa from the Gambia and Senegal in the west through the Volta, Niger and Chad basins to the Nile where populations of P. senegalus extend upstream as far as the Murchison Falls and Lake Mobutu (formerly Lake Albert).

Commercial importance: nil

Maximum recorded size: in Lake Turkana 47.5 cm TL

Polypterus bichir Geoffroy Saint-Hilaire, 1802

(Fig. 5.5)

Turkana name: nagiri

BOULENGER (2909) noted the presence of P. bichir in Lake Turkana. None was recorded from the area by subsequent workers but four specimens of 52-65 cm SL were obtained during the present investigations.

Diagnosis: the present species is easily distinguished from P. senegalus by the higher number of finlets in the dorsal fin, which in populations elsewhere ranges from 13 to 18 (cf 8-11 in P. senegalus). Fish from Lake Turkana had 15-16 finlets. Other differences in P. bichir include a somewhat depressed body form, a flat or only slightly convex interorbital space and relatively longer pectoral fins which usually extend posteriorly beyond the vertical to the first finlet.

Colouration: generally fawn with an irregular marbling of darker brown.

Food: BLACHE (1964) noted that in Lake Chad, P. bichir is piscivorous.

Distribution: Three out of the four specimens examined during the present investigations were caught by fishermen at Ferguson's Gulf, either in shore seines or gillnets, during April and May 1974. The fourth was collected in a channel at the mouth of the Kerio River during September 1973. It seems likely that these fish, all relatively large individuals, were stragglers, well out of the normal limits of their range which probably lies within the basin of the River Omo.

Commercial importance: nil

Maximum recorded size: in Lake Turkana 74 cm TL

Family Osteoglossidae

Genus Heterotis Muller, 1843

A monospecific genus belonging to a small but distinctive family of freshwater fish. Body strongly compressed with large scales each with a conspicuous mosaic pattern of sutures. Small conical teeth in a single series on the premaxillaries, maxillaries and dentaries. Villiform teeth on the entopterygoids and tongue. Pores of the lateral line system in grooves, particularly well developed and conspicuous on the head. Dorsal and anal fins of similar size, situated in the posterior half of the body. Unlike other osteoglossids, Heterotis is microphagous and is equipped with a unique helical suprabranchial organ on the 4th and 5th gill-arches which plays a role in the filtration of food.

Heterotis niloticus Cuvier, 1929

(Fig. 5.6)

Turkana name: dese

Heterotis niloticus was first collected from Lake Turkana by Zaphiro and McMillan in 1908 (BOULENGER, 1909). No further occurrences were recorded until MANN (1964) who notes that Mr R R McConnell of the Fisheries Department caught a specimen at Ferguson's Gulf in 1963. With the subsequent spread of the commercial gillnet fishery into the vicinity of the Kerio and Omo deltas, the species has been caught increasingly frequently in recent years.

Description: based on morphometric details in BOULENGER (1909) - body rather elongate and compressed. Head and snout rounded. Dorsal fin rays 32-37, anal fin rays 34-39. Caudal fin small, rounded. Pelvic fins inserted midway between the base of the pectoral fin and the origin of the anal fin. Lateral line scales 32-38. Scales between the lateral line and the origin of the dorsal fin 2 ½.

Colouration: olive brown, lighter on the ventral surface

Food: zooplankton, phytoplankton, grass seeds, small insects, etc.

Breeding: though not observed in Lake Turkana the spawning habits of Heterotis are well known. Breeding pairs construct circular nests of grass, approximately 1 metre in diameter in which the eggs are laid and tended until the young hatch.

Distribution: in Lake Turkana H. niloticus is virtually confined to the vicinity of the Omo and Kerio deltas (Fig. 5.7), the only regions where extensive areas of swamp vegetation are situated. Away from these two centres of distribution the only records obtained for this species during the present survey were for single fish at Ferguson's Gulf, Audache Lagoon and Koobi Fora (Fig.5.7).

Elsewhere H. niloticus is widespread throughout the soudanian region from the Gambia and Senegal, through the Volta, Niger and Chad basins to the Nile.

Commercial importance: H. niloticus has recently become of minor and local importance in the commercial fishery of Lake Turkana and a total of 17 tonnes wet weight caught during 1974 formed 0.47% of the entire commercial catch. Trends in the fishery at Kerio and at Todenyang between 1972 and 1974 are shown in Table 5.2 which demonstrates that a sharp fall in catch at Kerio has coincided with a steep rise in catches from the Omo delta. These dramatic changes in catch may not necessarily reflect changes in population density. The increase at Todenyang was probably due to an expansion of the fishery within the delta during 1974 combined with a decrease in stretched mesh size of gillnets from 7-8 inches to 5-6 inches (see Chapter 6) and the decrease at Kerio may have been due to a fall in mesh size below the optimum for this species.

Seasonal changes in H. niloticus catches from the Omo area during 1974 and 1975 are demonstrated by Figure 5.8. Similar trends are evident in the two years. Catches were generally high during the early months of the year in the pre-flood season and fell to low levels from the time of peak flooding in August and September onwards. During this period considerable areas of shallow swamp in the Omo delta were inundated. It seems likely that H. niloticus enter the swampy areas for the purpose of feeding and spawning and that under such circumstances gillnets would be relatively ineffective.

Maximum recorded size: in Lake Turkana 90 cm TL

Family Mormyridae

Mormyrid fish share a number of distinctive features which in spite of wide variation in body form render them easily recognisable. The skin on the head is thick, with well developed mucous glands, hiding much of the underlying pattern of bones, and covering the eyes with a transparent sheath. Teeth are always present but the form of the mouth varies greatly from species to species and is often tubular. The scales are small and cycloid, the caudal peduncle usually slender and well-defined. Muscles within the caudal peduncle are modified to form an electric organ which creates a weak electromagnetic field. The organ is believed to function as part of a special electrosensory system which facilitates location, orientation and communication in this group of fish.

Previously no mormyrid fish had been recorded from the Turkana basin but during the present survey two species, *Hyperopisus bebe* Gill and *Mormyrus kannume* L. were identified from the region of the Omo delta and a single specimen of *M. kannume* was collected from the permanent waters of the middle Turkwell at Katilo. Neither species was recorded from high salinity water in the actual lake although both are widespread under lacustrine conditions elsewhere. It seems highly probable that conductivities in Lake Turkana are high enough to render the electrosensory system useless and that the absence of Mormyrids from the main lake is due to this reason.

Hyperopisus bebe Lacépède, 1803

(Fig. 5.9)

Two individuals of 41 and 45 cm SL were recorded during the present survey. They were caught together in 4" surface set gillnets in open water, 5 m deep, 2.9 km south of the Dierheile branch of the Omo delta on the night of 18-19/X/74. The nets were set in a tongue of low salinity water with a conductivity of 150-172 µS/cm, only slightly higher than that of the main river.

Description: body compressed, elongated. Head rounded, mouth terminal, snout relatively short, its length twice the diameter of the eye. Teeth small, notched, 3-5 in the upper jaw, 5-6 in the lower jaw. Dorsal fin short with 12-16 rays situated posteriorly. Anal fin elongated with 58-68 rays. Lateral line scales 93-120.

Colouration: Lake Turkana specimens are dark brown, spotted finely with black above blending into yellow on the flanks and silvery yellow below. Blueish iridescence noticeable dorso-laterally.

Distribution: probably restricted to the River Omo, occurring as a rare straggler in the lake near the river mouth during the flood season.

Elsewhere widely distributed through the soudanian region from Senegal through the Volta, Niger and Chad basins to the Nile.

Commercial importance: an edible species but of no economic importance in view of its extreme rarity.

Maximum recorded size: attains a length of ca 50 cm TL

Mormyrus kannume Forsskål, 1775

(Fig. 5.10)

Turkana name: mkale

Only one specimen of M. kannume was caught in experimental nets during the present survey. The fish was caught in the permanent waters of the Middle Turkwell at Katilo, approximately 170 km upstream from the Lake. However, from 1973 onwards the species was taken in increasing numbers by fishermen from the region of the Omo delta and marketed as a sun-dried product at the local co-operative.

Description: body relatively long and compressed. Snout elongated to form a downward curving proboscis with the mouth situated at the tip. Length of snout up to 3 times its least depth. Dorsal fin long, with 57-75 rays, its origin situated above or slightly in front of the vertical to the pelvic fin. Anal fin relatively short with 18-21 rays, situated midway between the base of the pelvic fin and the tip of the caudal peduncle. Lateral line with 80-115 scales.

Colouration: fawn or olive brown above, lighter below

Distribution: frequent in the delta of the River Omo during the flood season. Absent from Lake Turkana as a whole but a separate and probably isolated population inhabits the middle reaches of the River Turkwell.

Elsewhere M. kannume extends throughout the Nile basin and occurs in Lakes Victoria, Kyoga, Mobutu (formerly Lake Albert), Edward and George.

Commercial importance: unlikely that M. kannume will assume more than minor local importance in the lower reaches of the River Omo as a commercial species. Data from Todenyang and Lowarangak co-operatives show that during 1973-75 the following wet weight of mormyrids were caught each year:

Year	Wet weight in tonnes
1972 (from May)	-
1973	0.1
1974	0.8
1975	0.1

Although all mormyrids examined at the co-operatives by competent observers were M. kannume, it is possible that Hyperopisus bebe and other hitherto unrecorded species of mormyrid were also included in the above totals.

Catches of mormyrids varied considerably from season to season with low numbers in the pre-flood periods increasing rapidly to a peak in the flood period between July and September each year (Fig. 5.11).

These data indicate an annual influx of mormyrid fish into the delta area during flooding. If, as suggested above, the elctro-sensory system of mormyrids is adversely affected by high salinities, the movement of fish into the delta may be correlated with the marked decrease in salinity which occurs in this region when the Omo is in spate.

Maximum recorded size: in Lake Turkana 58 cm FL

Family Gymnarchidae

Genus Gymnarchus Cuvier, 1829

Gymnarchus niloticus

(Fig.5.11)

Turkana name: lowarayame

The sole representative of the Gymnarchidae, a family closely related to the Mormyridae. As in mormyrid fish (see above) the caudal musculature has become modified to form a weak electric organ, part of an electrosensory system.

Gymnarchus niloticus was first collected from the north east corner of Lake Turkana in 1908 by Zaphiro and McMillan (BOULENGER, 1909). No individuals were caught by subsequent investigators nor in experimental nets set during the course of the present survey. Since 1972, however, this species has been taken in increasing numbers by fishermen in the vicinity of the Omo delta and marketed in a sun-dried condition at the local co-operative.

Description: body much elongated, eel-like, 7-11 times as long as deep. Snout rounded, mouth slightly subterminal and large with a single row of teeth along the edges of both jaws, 12-14 in the upper jaw, 22-28 in the lower. Eye very small. Dorsal fin with 180-230 rays extending along the entire length of the body. Anal, caudal and pelvic fins absent, the caudal region tapering to an obtuse point. Body covered with minute scales.

Colouration: brownish or blackish above, whitish below.

Distribution: confined to the Omo delta region and absent from the main lake.

Elsewhere distributed throughout the soudanian region of Africa from the Gambia and Senegal through the Niger, Volta and Chad basins to the Nile.

Commercial importance: as with M. kannume, the present species will probably never assume more than minor local importance within the restricted area of the lower Omo. The flesh of this species is however highly esteemed in many parts of Africa and it is often sold at a considerable premium. Co-operative data from Todenyang and Lowarangak show that the following quantities of G. niloticus were marketed each year:

Year	Wet weight in tonnes
1972	< 0.1
1973	4.7
1974	6.0
1975	1.9

Seasonal changes in the Gymnarchus fishery followed a similar pattern to that of the mormyrids with low catches during the pre-flood season, rising steeply with the onset of flooding to a peak between July and September (Fig. 5.13). Like mormyrids, G. niloticus probably penetrates downriver during the flood period as a result of a general fall in conductivity to levels suitable for the proper functioning of the electrosensory system.

Maximum recorded size: in Lake Turkana 99 cm TL

Family Characidae

Genus Hydrocynus Cuvier, 1819

Tiger fish are readily recognised by the single row of large acutely pointed, unicuspid teeth (tricuspid only in very small specimens), the teeth from one jaw interlocking with the teeth from the other when the mouth is shut. The body is relatively long and slender with cycloid scales. A small adipose fin is present and the dorsal fin is situated above the pelvic fin. Two species have been recorded from the Turkana basin.

Hydrocynus forskalii Cuvier, 1819

(Fig. 5.14)

Turkana name: lokel English name: Tigerfish

The occurence of H. forskalii in Lake Turkana was noted by BOULENGER (1909). Subsequent observations have proved that this species occurs abundantly throughout the lake. Detailed biological investigations are presented in a separate account (see page 753).

Description: based on ten fish of 18-58 cm SL: body 4.2-5.3 times as long as deep and 4.3-5.0 times the length of the head. Head 2.0-2.2 times as long as wide. Eye diameter 3.4-5.2 times in the length of the head (negative allometry). Interoribital width approximately equal to the length of the snout, 1.1-1.9 times the diameter of the eye. Pectoral fin 0.7-0.8 times the length of the head. Dorsal fin with II 10 rays, 0.9-1.1 times as long as the head. Anal fin rays III 11-12. Caudal peduncle 1.3-1.9 times as long as deep. Distance between snount and origin of dorsal fin 1.51-1.78 times the distance between the last dorsal fin ray and the adipose fin. Lateral line scales 48-52 (M=51), the first two often hidden between dermal elements of the pectoral girdle. Scales between lateral line and pelvic fin 2.

Colouration: silvery, often suffused with yellow and shot with a greenish iridescence, dorsal surface heavily pigmented with longitudinal lines of black pigment running along the entire length of the scale rows. The pattern extends onto the flanks gradually becoming less intense and ending at the level of the lateral line. Ventral surface whitish. Pectoral, pelvic and anal fins tinged with reddish orange. Lower lobe of caudal fin similarly but more intensely pigmented. The adipose fin is grey.

Food: chiefly small fish (see page 762)

Breeding: spawns within the lake although part of the population may undergo a breeding migration up the River Omo. Matures at ca 30 cm FL (see page 758). Juvenile stages are described on page 756.

Distribution: common throughout Lake Turkana both inshore and in surface waters offshore (see Figs. 8.8, 8.21 and 8.49). Shoals often seen breaking the surface of the open water on calm evenings.

Elsewhere extends throughout most of the soudanian region from Senegal through the Volta, Niger and Chad basins to the Nile, where it extends up river as far as Lake Mobutu (formerly Lake Albert). Also occurs in Lake Margherita.

Commercial importance: annual catches have risen in recent years from 233 tonnes wet weight in 1972 to 318 tonnes in 1974. Potential yields are probably much higher but the quality of *H. forskalii* is poor and an expanded fishery would necessitate the use of 3"-4" gillnets which would be deleterious to stocks of more valuable species (see page 380).

Maximum recorded size: in Lake Turkana 63 cm FL

Hydrocynus lineatus Bleeker, 1862

(Fig. 5.15)

This species was first collected by the 1930-31 Cambridge University Expedition (WORTHINGTON and RICARDO, 1936). A total of five fish (four of which ranged from 48 to 63 cm FL) were caught in open water on the east shore between Jarigole and Moite. The species has not been recorded by subsequent investigators and none was observed during the present survey. It is possible that in the Turkana basin this species is principally riverine in form and that ecological changes have occurred since 1931 which have tended to inhibit incursions of *H. lineatus* into the lake. A similar phenomenon is suggested by records of *Synodontis frontosus* and *Auchenoglanis occidentalis* which were collected from the Ferguson's Gulf area by MANN (1964) but were not observed outside the region of the Omo delta during the present study.

Description: based on data in GREENWOOD (1956): similar to *H. forskalii* but with a deeper body (3.25-4.50 times longer than deep) and with the dorsal fin situated more posteriorly. Thus the distance between the tip of the snout and the origin of the dorsal fin is 2.0-2.5 times the distance between the base of the last dorsal fin ray and the dorsal fin (cf 1.5-1.8 times in *H. forskalii*). Lateral line scales 45-48 (cf 48-53 in *H. forskalii*).

Colouration: similar to *H. forskalii* but with a black instead of a grey adipose fin.

Distribution: widespread in many parts of Africa including most of the soudanian region from Senegal to the Nile, Lake Tanganyika and the Katanga, Zambezi, Limpopo and Congo basins.

Genus *Alestes* Muller and Troschel, 1846

Slender or moderately slender silvery fish with cycloid scales. Teeth in upper jaw in two rows, the outer usually tricuspid, the inner more massive with many cusps. Lower jaw with an outer row of tricuspid teeth and an inner row represented by two unicuspid teeth adjacent to one another on the mid-line. Adipose fin present. Distal margin of anal fin markedly convex in mature males.

Alestes dentex (L) 1757

(Fig. 5.16)

The occurence of *A. dentex* in Lake Turkana was noted by BOULENGER (1909). None was collected by the 1930-31 Cambridge University Expedition (WORTHINGTON and RICARDO, 1936) but MANN (1964) obtained specimens from the vicinity of Longech Spit in September-October 1963. The species was caught locally in small numbers during the present survey, generally in association with *Alestes baremose*, a more common and widely distributed species which *A. dentex* closely resembles.

Description: body 3.5-4.8 times the maximum depth and 5-6 times the length of the head. Diameter of eye 3.4-4.1 times in the length of the head, approximately equal to the length of the snout. Dorsal fin rays II 8. Anal fin rays III 19-23 (M=21). Lateral line scales 45-50. Scales between the lateral line and the dorsal fin origin 8½-9½.

Colouration: silvery, with shading of dark pigment on the dorsal surface, whitish below. Silver often tinged with yellow. Bright lemon yellow on the eye, the pelvic fin, the anterior part of the anal fin and the distal half of the lower lobe of the caudal fin. Basal portion of caudal fin orange-red.

Diagnosis: distinguished from *A. baremose* by the following features:

Alestes dentex	*Alestes baremose*
Yellow pigment on eye, pelvic, anal and caudal fins	No yellow pigment on eye, pelvic, anal or caudal fins
Number of branched anal fin rays 19-23	Number of branched anal fin rays 22-27
Lobes of caudal fin equal in length	Lower lobe of caudal fin distinctly longer than upper
Tendency for slight concavity in dorsal profile of head in the region of the eyes	Dorsal profile of head always convex

Food: chiefly macrophytic plants, particularly *Potamogeton* but also epilithic algae scraped from rocks, and a small proportion of insects.

Breeding: probably similar to *A. baremose* with spawning migration up the Omo River but no definite proof. Matures at ca 30 cm FL.

Distribution: local in distribution, occurring in small numbers chiefly on the eastern side of the lake in sheltered bays with beds of *Potamogeton*. Rare in open water offshore.

Elsewhere widespread throughout the soudanian region from the Gambia and Senegal through the Volta, Niger and Chad basins to the Nile where it extends upriver as far as Lake Mobutu (formerly Lake Albert).

Commercial importance: valuable fisheries for *A. dentex* exist in other parts of Africa but in Lake Turkana the species will probably never make more than a slight contribution to the potentially important *Alestes* fisheries which would be based on *A. baremose*.

Maximum recorded size: in Lake Turkana 41 cm FL

Alestes baremose Joannis, 1835

(Fig. 5.17)

Turkana name: lelete

Alestes baremose was recorded from Lake Turkana by BOULENGER (1909). Large numbers were caught during the present investigations and the biology of this species has been studied in detail (see page 767).

Description: very similar to *A. dentex* in morphometry but with 22-27 branched anal fin rays (M=23-24, $\bar{x}$=23.8). For other distinctions between the two species see *Alestes dentex* above.

Colouration: silvery, with dark shading of melanophores on the dorsal surface, whitish below. No yellow on eyes, body or fins. Caudal fin tinged with red, most intense on lower lobe. Other fins clear.

Food: principally zooplankton (see page 783).

Breeding: anadromous with spawning migration into the River Omo during the flood season. Matures at ca 32-33 cm FL (see page 780).

Distribution: common, at times abundant throughout the lake, particularly in coastal waters. Concentrates in the Northern Sector during the flood season prior to migration.

Elsewhere distribution similar to that of *A. dentex* occurring throughout the soudanian region from Gambia and Senegal, through the Volta, Niger and Chad basins to the Nile where it extends upriver as far as Lake Mobutu (formerly Lake Albert).

Commercial importance: at present not caught in commercial quantities but potentially an important species (see page 767). Valuable fisheries for *A. baremose* exist in other parts of its range.

Maximum recorded size: in Lake Turkana, 46 cm FL

Alestes nurse Rüppell, 1832

(Fig. 5.18)

Alestes nurse was recorded from Lake Turkana by BOULENGER (1909). WORTHINGTON (1932) found the species abundant on the lake shore in the Ferguson's Gulf area and observed that adult fish were unusually small, reaching sexual maturity at about 4 cm FL and attaining a maximum size of 5 cm, compared with 20 cm elsewhere. He also noted the absence of dark markings on the caudal peduncle and behind the operculum which are normally found in this species. PELLEGRIN (1935) made similar observations on material from Lake Turkana and established a new subspecies, *A. nurse nana*.

Alestes nurse was collected in large numbers during the present survey. Previous observations regarding length at first maturity were confirmed but individuals up to 12 cm FL were recorded. Faint but distinct patches of melanophores were present, one on the caudal peduncle and the other on the flanks immediately behind the operculum.

Description: based on 30 fish of 3.2-4.9 cm SL: length 3.1-3.8 times the maximum depth and 3.5-3.8 times the length of the head. Eye 2.5 times in the length of the head, 0.84-1.07 times in the interorbital width and 0.56-0.78 times in the length of the snout. Dorsal profile of head convex. Caudal peduncle 1.07-1.47 times as long as deep. Pectoral fin 0.65-0.76 times the length of the head. Dorsal fin 0.78-0.89 times as long as the head. Dorsal fin rays II 8. Anal fin rays III 12 (f=8) more frequently III 13 (f=22). Lateral line scales 29-32 (M=30). Scales between lateral line and origin of dorsal fin 5½. Gillrakers 18-20 (M=19). Number of vertebrae 35-38 (M=37). Lower jaw with 8 outer and 2 inner teeth. Eight 4 or 5-cusped inner premaxillary teeth. Four to eight tricuspid outer premaxillary teeth, the flanking cusps of each tooth small and insignificant, the central cusps large and pointed but not drawn out into a slender fang.

Colouration: silvery with dark shading above, lighter below. Caudal fin tinged with red. In formalin-fixed specimens, body with extensive though fine peppering of melanophores on the dorsal surface and flanks, more intense on the caudal peduncle to form a black spot. A second spot often present on the flanks immediately behind the operculum.

Diagnosis: Alestes nurse closely resembles A. ferox and A. minutus, the recently discovered endemic species from Lake Turkana. Diagnostic criteria are discussed in the descriptions of the two species below.

Food: chiefly small insects and zooplankton (see page 1508).

Breeding: spawning occurs within the lake. Matures at a length of 3.5-4.0 cm FL.

Distribution: a littoral species, common on substrates of mud, sand or gravel in shallow inshore water throughout the lake. Often moves into rivers, including ephemeral rivers during the flood period.

Elsewhere A. nurse extends throughout the soudanian region from Senegal to the Nile where it occurs upriver as far as Lake Victoria. Also recorded from forest rivers in West Africa from Liberia to the Cameroun Republic.

Commercial importance: nil

Maximum recorded size: in Lake Turkana 12 cm FL but grows to over 20 cm FL elsewhere.

Alestes ferox sp. nov.

(Fig. 5.19)

This species together with Alestes minutus (see page 302) was discovered during the present investigations. Both forms are endemic to Lake Turkana and pelagic in distribution, restricted to the offshore waters where they are the fish chiefly responsible for the characteristic echo traces which constitute the midwater scattering layer (see page 637). The two species resemble Alestes nurse closely in morphology, squamation and metameric counts, differing principally in the shape of the head, dentition, breeding biology and in ecology. The present species is the largest of the three small Alestes occurring in Lake Turkana.

1978.5.16:1

Holotype. A male of 60 mm standard length (BMNH reg. no. available) in an oblique metre townet haul 1 km west of North Island at a lake depth of 38 m on 31/8/1973. The specimen was fixed in formalin.

Paratypes.

1978.5.16:2-30

(i) Twenty nine formalin-fixed specimens (BMNH reg. nos. available) 25-81 mm SL caught 4 km east of Longech Spit at a lake depth of 29 m.

1978.5.16.31-36

(ii) Six alizarin stained fish preserved in glycerol (BMNH reg. nos. available) of 39-49 mm SL from the same locality.

Description: based on the holotype and on 35 paratypes of 25-81 mm SL. Length 3.1-4.0 times the maximum depth and 3.0-3.4 times the length of the head. Eye 2.6-3.2 times in the length of the head, 0.5-0.7 times in the interorbital width (measured across the frontals) and 0.7-0.9 times in the length of the snout. The premaxilla is elongated compared with other *Alestes* spp. to give the snout a distinctive muzzle-like appearance. Dorsal profile of head partly concave. Mouth large. Caudal peduncle 1.1-1.4 times as long as deep. Pectoral fin 0.5-0.7 times the length of the head. Dorsal fin 0.6-0.8 times as long as the head with II 8 rays. Anal fin rays usually III 13 (f=30), more rarely III 14 (f=3) or III 12 (f=2). In mature males the central rays of the anal fin are elongated and expanded as is usual in *Alestes* and related genera. The scales are thin and readily detached in the course of capture in trawl or metre townet hauls. Only the holotype was caught with the scales intact. The squamation was as follows:- lateral line scales 36, scales between the lateral line and the mid-dorsal line near the origin to the dorsal fin 6½, scales between the lateral line and the mid-ventral line 3½, scales round the caudal peduncle 12. Gillrakers 19-23 (M=21). Number of vertebrae 35-38 (M=37).

The *teeth* are unusually long, sharply pointed and fang-like for an *Alestes*. *Outer row* of *premaxilla* formed by 8, more rarely 10, unicuspid teeth situated anteriorly. Each tooth consists of a squat cylindrical base produced distally into a slender, curved caniniform cusp. The central teeth of the outer row tend to point forwards and downwards and the more lateral teeth downwards and backwards. Due to their position on the anterior margin of the premaxilla, the teeth often protrude forwards beyond the fleshy part of the snout and the upper lips, and are visible when the fish is viewed from above. Eight to ten pluricuspid teeth form the *inner row* of the *premaxilla*. The four anterior teeth, which have noticeably bulbous bases, are more massive than the adjacent teeth on the outer row. Each inner anterior tooth bears a well developed backward-curving caniniform cusp flanked on each side by two insignificant conical cusps, the outer of which are often barely discernable. The posterior teeth of the inner premaxillary row, which are inserted on the lateral margin of the jaw behind the row of outer teeth, are smaller than the anterior pluricuspids. The principal cusps of the posterior teeth are also caniniform but the subsidiary cusps, which usually number 2 or 3, are larger than those of the anterior premaxillary series, and the hind teeth thus appear less fang-like.

The *lower jaw* is furnished with an *outer row* of 8-12 (usually 10) teeth bearing 3-5 sharp cusps. As in the pluricuspid teeth of the upper jaw, the principal cusp is acutely pointed, backward curving and caniniform, up to six times the length of the largest subsidiary cusp. The size of the teeth of the lower jaw tends to decrease posteriorly and the series terminates on either side with a relatively small and insignificant tooth. Two strongly decurved, backward directed, hook-like unicuspid teeth lying adjacent to one another, form the inner tooth row of the lower jaw.

Although the dentition of A. ferox, with the series of fang-like teeth on both jaws, superficially resembles Hydrocynus spp., the teeth do not interlock in the closed position. In A. ferox the upper teeth shut forward of the lower teeth and the fish is thus noticeably prognathous.

Summary of morphometric data: based on measurements obtained from the holotype and 29 formalin-fixed paratypes ranging from 25-81 mm SL. The measurements have been expressed as a percentage of the standard length.

	Mean	Standard deviation	Range
Maximum depth	29.2	1.52	24.8-32.4
Length head	31.1	1.18	29.0-33.3
Width head	15.3	0.72	14.0-16.9
Diameter eye	10.9	0.70	9.6-12.4
Interorbital width*	6.1	0.39	5.2- 7.0
Length snout	8.3	0.38	7.6- 9.0
Length pectoral fin	19.1	1.20	16.0-21.0
Length dorsal fin	21.9	0.87	20.5-23.5
Length caudal peduncle	12.2	0.93	10.0-13.4
Depth caudal peduncle	9.8	0.38	8.9-10.5

*bony interorbital width measured across frontals

Colouration: in living specimens, pale fawn with silver scales, darker on the dorsal surface. Both lobes of the caudal fin marked with red chromatophores which are interspersed with yellow chromatophores on the lower lobe. In formalin-fixed specimens the dorsal surface is lightly patterned with melanophores, heavier in a band on the mid-dorsal line. Characteristic patches of black pigment are present on the snout, on the lower jaw and on the mid-lateral portion of the caudal peduncle. In some specimens, a small but distinct black spot is present on the flanks posterior to the operculum. Distal margin of caudal fin with broad edging of black pigment.

Diagnosis: readily distinguished from other Alestes by the sharply pointed fang-like teeth and by the muzzle-like prognathous snout (see Fig. 5.20a). The unusual dentition has probably evolved as a response to the pelagic habits of A. ferox in Lake Turkana, resulting in the adoption of a specialised diet, which in larger individuals includes a high proportion of prawns and small fish.

In collections of small fish from Lake Turkana *A. ferox* is also distinguished from *A. nurse* by the lack of heavy pigment in the region of the horizontal myoseptum. Easily separated from *A. minutus* by the presence of black pigment on the snout, mid-dorsal line, caudal peduncle and caudal fin. Matures at a larger size than either the Lake Turkana population of *A. nurse* or *A. minutus*.

Food: chiefly prawns, zooplankton and insects with an increasing proportion of small fish in larger individuals (see Chapter 12, page 1510).

Breeding: spawns within the lake. Matures at 6-8 cm FL (see Chapter 9, page 832).

Distribution: endemic to Lake Turkana. A pelagic species, at times abundant, occurring in the open waters throughout the lake. During daylight hours situated in the midwater scattering layer (see page 831). Disperses throughout the surface layers after dark and may occasionally occur inshore on steeply-shelving coastlines.

Commercial importance: a dominant species in terms of standing stock (see Chapter 8, page 606) but due to small size, unlikely to be of commercial importance unless an industrial fishery develops.

Maximum recorded size: 12 cm FL

Alestes minutus sp. nov.

(Fig. 5.20)

This is the smaller of the two endemic *Alestes* occurring in the open waters of Lake Turkana.

1978.5.16:37

Holotype. A female of 26 mm standard length (BMNH reg. no. available) caught in an oblique metre townet haul 5 km north west of Ilaret at e. a lake depth of 8 m on 7/8/1975.

Paratypes

1978.5.16:38-42

(i) Five formalin-fixed specimens (BMNH reg. nos. available) 26-28 mm SL from the same locality and sample as the holotype

1978.5.16:49-58

(ii) Ten formalin-fixed specimens (BMNH reg. nos. available) 26-30 mm SL east of Longech Spit at a lake depth of 30 m

1978.5.16:43-48

(iii) Six formalin-fixed specimens (BMNH reg. nos. available) 21-25 mm SL from 5 km north east of Longech Spit at a lake depth of 25 m

1978.5.16:59-64

(iv) Six alizarin stained fish preserved in glycerol (BMNH reg. nos. available) 28-33 mm SL from Kerio Bay at a lake depth of 10 m

Description: based on the holotype and on 27 paratypes of 21-33 mm SL. Body compressed, its length 3.3-3.8 times the maximum depth and 3.2-3.7 times the length of the head. Eye 2.3-2.8 times in the length of the head, 0.5-0.8 times in the interorbital width and 0.5-0.6 times in the length of the snout. Mouth superior, slightly subterminal. Caudal peduncle 1.0-1.2 times as long as deep. Pectoral fin 0.5-0.7 times the length of the head. Dorsal fin 0.6-0.8 times the length of the head with II 8 (f=27) rarely II 7 (f=1) rays. Anal fin rays III 13 (f=25) rarely III 12 (f=2) or III 14 (f=1). Scales exceptionally delicate and easily detached, a high proportion missing from all specimens examined. Approximately 31 scales in the lateral line and 5 ½ between the lateral line and the origin of the dorsal fin. Gillrakers 17-19 (M=18). Number of vertebrae 36-38 (M=37).

Premaxilla with 8, more rarely 6 or 7 small teeth in the outer row, usually unicuspid and conical. Occasional tricuspid teeth with two short lateral pointed cusps arising near the apex of the main cusp also noted from time to time in a series of otherwise conical teeth. Eight 5- or 6-cusped inner premaxillary teeth, each broad and somewhat compressed, with the acutely pointed cusps graduated in size forming a regular crest with the largest in the centre. Lower jaw with 8, more rarely 6 or 7 outer 4- or 5-cusped teeth which decrease markedly in size posteriorly. The anterior teeth of the row larger and stouter than the pluricuspid premaxillary teeth, with the principal cusps acutely pointed and backward-curving. Inner row or lower jaw represented by two conical teeth placed anteriorly close together on either side of the mid-line.

Summary of morphometric data: based on measurements obtained from the holotype and 21 formalin-fixed paratypes ranging from 21 to 30 mm SL. The measurements have been expressed as a percentage of the standard length.

	Mean	Standard deviation	Range
Maximum depth	28.1	1.07	26.6-30.7
Length head	29.8	1.26	27.1-31.7
Width head	15.4	0.84	13.9-17.1
Diameter eye	11.4	0.59	10.1-12.6
Interorbital width*	6.5	0.48	5.6- 7.3
Length snout	6.4	0.33	5.9- 7.3
Length pectoral fin	18.1	1.01	16.3-20.3
Length dorsal fin	21.5	1.01	19.3-23.4
Length caudal peduncle	10.8	0.43	9.7-11.4
Depth caudal peduncle	9.6	0.34	9.0-10.4

*bony interorbital width measured across frontals

Colouration: pale fawn with silvery scales. Fins clear. In formalin-fixed specimens pigmentation very light, confined chiefly to a cluster of melanophores on the dorsal surface of the head and a faint mid-dorsal line along the body. In well-marked specimens an ill-defined black lateral spot on the caudal peduncle and a faint mid-lateral band on the body are also present.

Diagnosis: distinguished from Alestes nurse by the shorter snout, slightly larger eye and narrower interorbital space (see Fig. 5.20a) The mouth in this species is noticeably superior and subterminal (cf terminal in A. nurse) and the predominance of unicuspid outer maxillary teeth is in marked contrast to A. nurse where the corresponding teeth are invaribaly tricuspid. Alestes minutus also lacks the relatively heavy pigmentation of A. nurse. Compared with A. ferox, the present species is a much smaller fish, and adults of 2-3 cm FL are easily separated from juvenile *A. ferox* of similar size by the shorter snout lacking the black pigmented spot, fang-like teeth and muzzle-like shape characteristic of the larger species.

Food: chiefly zooplankton with occasional small insects (see Chapter 12, page 1509).

Breeding: spawns within the lake. Matures at an exceptionally small size for an *Alestes* and breeds at a length of 2.5-3.0 cm FL (see Chapter 9, page 835).

Distribution: a pelagic species, usually occurring together with *A. ferox*, widespread throughout the open waters of the lake. Situated in the midwater scattering layer during the hours of daylight. Disperses throughout the surface waters after dark. Endemic to Lake Turkana.

Commercial importance: open water surveys indicate that in terms of biomass, *A. minutus* is by far the most important species of fish in the lake (see Chapter 8, page 607). Due to its small size *A. minutus* is, however, unlikely to be commercially important unless an industrial fishery is developed in Lake Turkana.

Maximum recorded size: 3.7 cm FL

Alestes macrolepidotus Cuvier and Valenciennes, 1849

(Fig. 5.21)

The first specimen from the Turkana basin was collected in the River Omo by Zaphiro and McMillaan in 1908 (BOULENGER, 1909). Subsequently two individuals were obtained from the River Omo by the 1932-33 Mission Scientifique de l'Omo (PELLEGRIN, 1935). Not caught during the present survey but a specimen of ca 20 cm FL was observed swimming slowly at the surface (in the manner characteristic of this species) in the River Omo at Lochui, 10 km upstream from the mouth of the delta.

Description: head strikingly flattened above the ventral profile rising steeply from the belly to the tip of the snout. Dorsal fin rays II 8, anal fin rays III 12-14. Scales large, 22-24 in the lateral line, 4½ between the lateral line and the origin of the dorsal fin and 1 or 2 between the lateral line and the pelvic fin.

Colouration: dark olive-green or brown above, silvery on the flanks and below. Caudal peduncle marked laterally with large blackish spot. Fins tinged with red or pink.

Distribution: probably restricted to the River Omo and its delta but may occur as a rare vagrant in the extreme north of Lake Turkana.

Elsewhere widely distributed throughout the soudanian region from Senegal, through the Volta, Niger and Chad basins where it extends upriver to Lake Mobutu (formerly Lake Albert). Also occurs in the Congo basin.

Commercial importance: none in Lake Turkana

Maximum recorded size: grows to at least 50 cm FL

Genus Micralestes Boulenger, 1899

Diminutive, moderately slender characin fish, similar in morphometry to small species of Alestes. Distinguished by the inner teeth of the upper jaw which have compressed or flattened bases compared with thick expanded bases in Alestes. Small adipose fin present.

Micralestes acutidens Peters, 1852

(Fig. 5.22)

Micralestes was first collected from the Turkana basin (River Omo) by Professor Neumann (BOULENGER, 1909). Although not recorded previously from the actual lake, the species occurred commonly in collections of fish from inshore and offshore sites in the northern basin during the course of the present project.

Description: based on 15 fish of 3.2-3.6 cm SL: length 3.2-3.6 times the maximum depth and 4.0-4.6 times the length of the head. Eye 2.5-2.7 times in the length of the head, 0.81-0.87 times in the interorbital width and 0.79-0.96 times in the length of the snout. Dorsal fin rays II 8. Anal fin rays III 14-15. Lateral line scales 27-19 (M=28). Four and a half scales between the lateral line and the origin of the dorsal fin. Upper jaw with 6-8 outer tricuspid teeth and 8 inner 4 to 7-cusped teeth. Lower jaw with 8 outer 4 to 7-cusped teeth and two inner simple conical teeth. The cusps of each pluricuspid tooth are arranged in a line with the largest in the centre.

Colouration: body straw-coloured with a broad silvery mid-lateral stripe. Caudal fin often tinged with red. The dorsal fin often lacks the black tip which is characteristic of populations of this species elsewhere. In formalin-fixed specimens the silvery mid-lateral band is replaced by a conspicuous black stripe.

Diagnosis: distinguished from small Alestes, which it superficially resembles, by the form of the teeth and in preserved material by the black lateral stripe.

Food: chiefly zooplankton, though stomachs frequently filled with the colonial blue-green alga Microcystis aeruginosa (see page 1510).

Breeding: spawns within the lake. Matures at a size of 3.0-3.5 cm FL .

Distribution: common in the shallow waters of Ferguson's Gulf. Otherwise chiefly restricted to the northern end of the lake where it occurs both inshore and at moderate depths in mid-lake.

Elsewhere widely distributed in the soudanian region from the Volta through the Niger and Chad basins to the Nile. Also recorded from the Congo, Zambezi and Limpopo basins.

Commercial importance: nil

Maximum recorded size: in Lake Turkana 4.5 cm FL

Family Citharinidae

Genus Citharinus Cuvier, 1817

Body short and deep, strongly compressed. Scales cycloid. Adipose fin large, basal portion at least covered with scales. Mouth broad, terminal or slightly subterminal with a single row of minute pointed teeth.

Citharinus citharis Geoffroy Saint-Hilaire, 1809

(Fig. 5.23)

Turkana name: gage

This species was first recorded from Lake Turkana by WORTHINGTON (1932) who found that the material was in certain respects intermediate between C. citharus and C. latus M. and T. from the lower Nile. In squamation, fin ray counts and eye proportions, the Turkana material approached C. citharus but the depth of body and width of head resembled C. latus more closely. On the basis of these characteristics Worthington established a new subspecies for the Lake Turkana form, C. citharinus intermedius Worthington. Although the species was caught in large numbers by commercial gillnets during the initial period of the present project, very few were taken in experimental nets. An account of the biology is given on page 789.

Description: based on morphometric data for fish ranging from 23 to 31 cm SL provided by WORTHINGTON (op. cit.). Length 1.6-1.9 times the maximum depth and 3.2-3.25 times the length of the head. Head 1.9-2.0 times as long as broad. Eye 4.5-5.2 times in the length of the head. Dorsal fin with 19-20 rays (4-6 unbranched). Anal fin with 26-29 rays (3 unbranched). Lateral line scales between the lateral line and the origin of the dorsal fin 23-25.

Colouration: body silver, darker above with greenish sheen. Pelvic fin, anal fin and lower lobe of the caudal fin orange-red.

Diagnosis: the combination of a deep, compressed body, large adipose fin and relatively small cycloid scales should prevent confusion with other species in the Turkana basin.

Food: microphagous, feeding on benthic algae on soft substrates (see page 789)

Breeding: anadromous, migrating up the River Omo to spawn during the flood season. Matures at approximately 45-50 cm FL (see page 791).

Distribution: confined to inshore waters in Lake Turkana on finer substrates within the 10 metre contour. Most plentiful in the Northern Sector of the lake.

Elsewhere widely distributed throughout the soudanian region from the Gambia and Senegal, through the Volta, Niger and Chad basins to the Nile where it extends upriver as far as Lake Mobutu (formerly Lake Albert).

Commercial importance: formerly the dominant species in the commercial fisheries of Lake Turkana but failure in recruitment (see page 796) has resulted in a dramatic fall in catch from 3040 tonnes wet weight in 1970 to 10 tonnes in 1975.

Maximum recorded size: in Lake Turkana 65 cm FL

Family Distichodontidae

Genus Distichodus Muller and Troschel, 1845

Body deep or moderately deep, compressed. Scales ctenoid. Adipose fin large, covered with scales. Mouth rather small with small bicuspid teeth, usually two rows in each jaw.

Distichodus niloticus (L) 1762

(Fig. 5.24)

Turkana name: golo

Distichodus niloticus was first collected from Lake Turkana by Donaldson Smith in 1898 (BOULENGER, 1909). During the present survey relatively few fish have been caught in experimental gear and most information has been derived from commercial gillnet catches. The biology of D. niloticus is discussed on pages

Description: length 2.5-3.4 times the maximum depth and 3.2-5.1 times the length of the head. Diameter of eye 3-6 times in the length of the head. Both head and eye are relatively larger in smaller fish. Dorsal fin with 22-26 fin rays (3-6 unbranched). Anal fin with 13-15 rays (3-4 unbranched). Scales extending well over the base of the caudal fin, 99-110 in the lateral line and 18-20 between the lateral line and the origin of the dorsal fin.

Colouration: dorsal surface of body and head dark silver-grey merging into whitish on the belly.

Diagnosis: the presence of ctenoid scales (which feel rough and abrasive to the touch) combined with bicuspid teeth and adipose fin should prevent confusion with other species in the Turkana basin.

Food: benthic invertebrates, particularly ostracods (see page 843).

Breeding: anadromous, migrating up the River Omo to spawn during the flood season. Matures at approximately 58 cm FL (see page 844).

Distribution: confined to the coastal waters of the lake within the 15 metre contour. Most plentiful in the northern basin and rare or absent on precipitous coastlines in the south.

Elsewhere confined to the Nile basin extending upriver as far as Lake Mobutu (formerly Lake Albert).

Commercial importance: formerly the second most important species in the Turkana gillnet fishery but in recent years the catch has declined from 480 tonnes wet weight caught in 1972 to 84 tonnes in 1975.

Maximum recorded size: in Lake Turkana 99 cm FL

Family Cyprinidae

Genus Labeo Cuvier, 1817

Body moderately elongated with cycloid scales. Mouth large, inferior. A flap of skin, the rostral flap, hangs down from the snout in front of the upper lip. Lips well developed. Jaws toothless but with horny cutting edges.

Labeo horie Heckel, 1846

(Fig. 5.25)

Turkana name: chibule

Labeo horie was first collected from Lake Turkana by the 1930-31 Cambridge University Expedition (WORTHINGTON and RICARDO, 1936). The species was also recorded by PELLEGRIN (1935) in material preserved by the 1932-33 Mission Scientifique de l'Omo. During the present investigations L. horie was caught commonly in coastal waters of the lake and a detailed account of the biology is given on pages 803 to 815

Description: based on 15 fish of 12-45 cm SL. Length 3.3-5.0 times the maximum depth and 4.2-6.0 times the length of the head. Diameter of eye 3.8-5.5 times in the length of the head showing negative allometry. Mouth subterminal, lips rather thin and crenellated. Barbel small, hidden in skin folds. Snout rounded. Dorsal fin rays IV 12-15 (M=13). Anal fin rays III 5. Lateral line scales 42-44 (M=43). Scales between lateral line and dorsal origin 7½ (f=10) or 8½ (f=4).

Colouration: scales patterned with green or bluish green and brown above, often with greenish, rose pink or golden iridescence. Body yellowish or silvery-white below. Fish below 6.5 cm FL with a round black spot on the horizontal myoseptum between the pectoral fin and the origin of the dorsal fin, and a second spot on the end of the caudal peduncle. Fins often with pinkish flush.

Diagnosis: easily recognised from other species which occur regularly in Lake Turkana by the form of the toothless subterminal mouth, by the relatively high number of dorsal fin rays and by the scale counts. Labeo cylindricus Peters, known from the upper reaches of both the Omo and Turkwell/Kerio systems might occur as a rare straggler to the lake. It differs from L. horie in a number of features including a more massive, fleshy and somewhat swollen snout, 35-39 lateral line scales and only III 8-10 dorsal fin rays.

Food: chiefly epibenthic algae and organic detritus (see page 803).

Breeding: anadromous, mature fish concentrating in the mouths of rivers, both the major and also ephemeral rivers such as the Kalakol, Kataboi and Tula Bor, during periods of spate. Post larvae and juveniles are common in the shallows of the lake after successful spawning. Matures at ca 55 cm FL (see page 804).

Distribution: common inshore species, generally distributed over soft substrates within the 10 metre contour, occasionally down to 20 metres.

Elsewhere restricted to the Nile basin extending upriver as far as Lake Mobutu (formerly Lake Albert).

Commercial importance: a valuable commercial species which replaced Citharinus citharus as the dominant species in the Turkana gillnet fishery between 1972 and 1974 when the annual catch of L. horie rose from 586 tonnes wet weight to 1034 tonnes.

Maximum recorded size: in Lake Turkana 86 cm FL

Genus Barbus Cuvier and Cloquet, 1816

Body somewhat compressed. Scales cycloid with parallel or concentric striae. Lateral line usually present, dipping below the horizontal myoseptum in the centre of the body but rising posteriorly to run along the middle of the caudal peduncle. Mouth variable in size, protractile and with lips. Two pairs of barbels usually present but one or both absent in some species. Dorsal fin rays III 6-11. The third simple dorsal ray is ossified in some species to form a spine. Anal fin rays III 4-7, usually III 5. A very large genus represented by several hundred species.

Barbus bynni Forsskål, 1775

(Fig. 5.26)

Turkana name: momwara

Barbus bynni was first recorded from Lake Turkana by PELLEGRIN (1905) as *B. meneliki* Pell. which BANISTER (1973) has shown to be synonymous with *B. bynni*. The present species belongs to the group of larger *Barbus* which have parallel striae on their scales. During the course of the present survey *B. bynni* was frequently encountered and a detailed study of its biology is given on pages 817 to 827.

Description: based on 24 fish of 11-43 cm SL: body rising to a noticeable peak at the origin of the dorsal fin. Length 3.0-3.8 times the maximum depth and 3.5-4.2 times the length of the head. Eye 3.0-5.4 times in the length of the head (negative allometry). Snout somewhat acutely rounded, its length 1.0-2.0 times the diaameter of the eye. In a small proportion of large fish of over 60 cm FL (not included in these measurements) the snout was greatly enlarged, projecting forward as a smooth rounded proboscis, 2-3 times its normal length. Dorsal fin with a long stout tapering spine 1.27-1.74 times the length of the head. Dorsal fin rays IV 9 rarely IV 8 or IV 10. Anal fin rays III 5. Lateral line scales 28-37. Scales between lateral line and the origin of the dorsal fin 6½ . Scales round caudal peduncle 14-16.

Colouration: variable. Upper parts greyish with silver iridescence or brownish to greenish yellow with golden iridescence. Underparts whitish or pale yellow. Fins greyish, pinkish or golden yellow. Top of snout frequently with chalky white patch in fish over ca 30 cm FL.

Diagnosis: A further species of large *Barbus*, *B. intermedius intermedius* occurs in the upper reaches of both the Omo and the Kerio/Turkwell river systems and may subsequently prove to occur as a rare vagrant in Lake Turkana. Compared with *Barbus bynni*, the riverine species has a less angular body profile and a considerably shorter dorsal fin, the length usually less than that of the head.

Food: chiefly benthic including ostracods, chironomid larvae and molluscs (see page 825).

Breeding: anadromous, undergoing a spawning migration into the River Omo during the flood season. Matures at 50 cm FL (see page 824).

Distribution: demersal species, well distributed over soft and hard substrates throughout the lake. Most numerous in shallow water within the 20 m contour but juveniles tend to extend into deeper water (see page 820).

Elsewhere extends over much of the Nile basin occurring upstream as far as Lake Mobutu (formerly Lake Albert). Also present in the region of Lake Abaya in the rift valley to the north east of Lake Turkana.

Commercial importance: a valuable species in the Turkana gillnet fishery. The annual catch of *B. bynni* rose considerably between 1972 and 1974 from 87 tonnes wet weight to 442 tronnes.

Maximum recorded size: in Lake Turkana 89 cm FL

Barbus turkanae sp. nov.

(Fig. 5.27)

This species was first collected in May 1972 when the deeper waters of Lake Turkana were sampled by bottom trawl for the first time.

1978.5.16:65

Holotype. A formalin-fixed specimen, 38 mm standar length (BMNH reg. no. available) from 6.5 km north west of Central Island, on or near the bottom at a depth of 45 m.

Paratypes.

1978.5.16:79-84

(i) Six formalin-fixed specimens (BMNH reg. no. available) 32-41 mm SL, from the same locality as the holotype

1978.5.16:66-78

(ii) Thirteen formalin-fixed specimens (BMNH reg. no. available) 36-42 mm SL, from 13 km west of Allia Bay at a depth of 45 m

1978.5.16:85-90

(iii) Five alizarin stained specimens in glycerol (BMNH reg. no. available) 30-38 mm SL.

Description: based on the holotype and 24 paratypes, 32-42 mm SL. Body somewhat compressed, the length 2.9-3.9 times the maximum depth and 3.1-3.6 times the length of the head. Predorsal profile convex with a noticeable nuchal hump. Snout 0.78 to equal the diameter of the eye, bluntly pointed in lateral aspect, more rounded when viewed from above. Mouth relatively small, subterminal, barbels absent. Eyes inclined noticeably upwards, 2.9-3.4 times in the length of the head. Pitlines of the *Beirabarbus* pattern (GREENWOOD, 1962) are present on the side of the snout, cheeks, operculum, and in the interorbital region. Pectoral fin 0.64-0.76 times the length of the head, the tip falling short of the pelvic origin. Last simple dorsal ray smooth, flexible, 0.85-0.98 times the length of the head. Dorsal fin rays III 8 (f=24), rarely III 9. Anal fin rays III 5. The pelvic origin lies between the verticals to the last simple and first branched dorsal rays. Caudal peduncle relatively elongated, 1.4 to 1.7 times as long as deep. The lateral line dips to a maximum of slightly less than half a scale row below the horizontal myoseptum in the anterior third of the body: the two converge posteriorly near the vertical to the pelvic origin. Scales radially striated. The lateral line scales, which are relatively tall and narrow on the anterior third of the body, number 22 (f=2), 23 (f=7), 24 (f=8) or 25 (f=1) not including the two scales overlapping the base of the caudal fin. Three and a half scales between the lateral line and the dorsal origin, 3½ (f=19) or rarely 4½ (f=1) between the lateral line and the mid-ventral line in front of the pelvic origin, and 2 scales between the lateral line and the pelvic origin. Nine (f=9) or 10 (f=11) scales around the caudal peduncle. The lower limb of the first gill arch with 6 or 7 gillrakers in five fish examined. Vertebrae 31 (f=1) or 32 (f=4).

Summary of morphometric data based on the holotype and 19 formalin-fixed paratypes of 32-42 mm SL. The measurements are expressed as a percentage of standard length.

	Mean	Standard deviation	Range
Maximum depth	30.7	1.65	25.7-34.7
Head length	29.3	1.14	27.7-32.3
Diameter eye	9.3	0.42	8.9-9.9
Interorbital width	9.6	0.51	8.5-10.3
Length snout	9.0	0.53	8.2-10.0
Length pectoral fin	20.6	1.36	20.0-21.8
Length dorsal fin	27.1	0.61	25.8-28.8
Length caudal peduncle	20.6	0.89	19.5-22.7
Depth caudal peduncle	13.4	0.58	12.1-14.7

Colouration: in living specimens generally pale silvery, the caudal fin tinged with pink in a small proportion of specimens examined. In formalin fixed specimens body peppered dorsally and dorso-laterally with fine melanophores, more intense along the mid-dorsal line. Dorsal scales each outlined with heavier marginal pigment forming a pattern extending laterally to the lateral line. A slender vertical bar of pigment, bisected by the lateral line, is present on the pocket of each lateral line scale. Such vertical bars are particularly noticeable on the more anterior scales. With the exception of occasional melanophores on the pockets of the scale row below the lateral line, the ventral surface is generally pigment-free. A narrow band of melanophores is always present on the mid-ventral line extending from the anal fin. The snout bears a conspicuous black lateral streak. Anterior margin of dorsal fin noticeably black due to dense pigment on the three simple rays. Remainder of dorsal fin with a light scattering of fine melanophores more concentrated near the distal margin. Outermost rays of caudal fin both marked with moderately heavy black pigment. Caudal fin rays otherwise lightly marked with a uniform scattering of fine melanophores. Anal, pectoral and pelvic fins very lightly pigmented with a few scattered melanophores, absent altogether in poorly marked individuals.

Diagnosis and affinities: in most respects Barbus turkanae is a typical member of the subgenus Enteromius, including pigmentation, squamation and the characteristic pore lines on the head. It differs from other members of the subgenus, with the exception of Barbus anema Boulenger, in the absence of barbels. The new species is obviously closely related to Barbus anema, a soudanian species, from which it may be distinguished by the relatively longer caudal peduncle (1.4-1.7 times as long as deep cf 1.1-1.5 in B. anema).

Food: chiefly benthic invertebrates including ostracods, caridea, naucorids, chironomid larvae and gastropods (see Chapter 12 page 1511).

Breeding: spawns within the lake. Matures at ca 3 cm FL.

Distribution: endemic to Lake Turkana. Confined to the deeper waters of the lake below the 10 metre contour. Ubiquitous on finer substrates below the 25 metre contour.

Commercial importance: nil

Maximum recorded size: 4.8 cm FL

Barbus werneri Boulenger, 1905

(Fig. 5.28)

Barbus werneri was first collected from Lake Turkana by Donaldson Smith in 1898 (BOULENGER, 1911). Further material was obtained from the River Omo and its delta by the 1932-33 Mission Scientifique de l'Omo (PELLEGRIN, 1935). Subsequent investigators have not recorded this species from the actual lake, but during the present survey populations of B. werneri were found inhabiting permanent pools in both the Kalakol and Kataboi rivers which empty directly into the lake across the coastal plains. The pools were situated in the hills from five to ten kilometres inland and it seems likely that during periods of spate the fish made at least temporary incursions into the shallows of the lake.

Description: based on four fish of 4.0-5.2 cm SL from the Kataboi Gorge. Length 3.3-3.4 times the maximum depth and 3.3-3.7 times the length of the head. Eye 3.3-3.5 times in the length of the head and 1.0-1.1 times in the length of the snout. Barbels relatively long, the anterior 0.69-0.73 times the diameter of the eye and the posterior 1.23-1.43 times this diameter. Dorsal fin rays III 8, anal fin rays III 5. Caudal peduncle 1.25-1.45 times as long as deep. Lateral line scales 26-29. Scales between the lateral line and the origin of the dorsal fin 4 ½ . Scales round caudal peduncle 13-14.

Colouration: Silvery, the body marked with 2 or 3 mid-lateral spots. In formalin-fixed specimens the round black lateral spots are the most conspicuous feature. The first two lie on the horizontal myoseptum in the anterior half of the body and the third on the tip of the caudal peduncle. In specimens with only two spots, the central spot is missing.

Breeding: entire life cycle probably spent in riverine pools.

Distribution: principally riverine in distribution. Recorded from the Omo system and noted upriver in the Turkwell/Kerio system during the present project. In the vicinity of the main lake inhabits permanent pools in ephemeral rivers.

Elsewhere occurs in the Chad and Nile basins and in the region of Lake Abaya.

Commercial importance: nil

Maximum recorded size: 6.5 cm FL

Genus Barilius Hamilton Buchanan, 1822

Small, rather slender cyprinid fish, body moderately compressed. Lateral line dips low to run parallel with the ventral outline of the body. Mouth large, terminal, oblique and without fleshy lips. Dorsal fin with 7-10 branched rays, originating approximately midway between the tip of the snout and the extremity of the vertical to the origin of the anal fin.

Barilius niloticus Joannis, 1835

(Fig. 5.29)

Barilius niloticus was first collected in the Turkana basin by Professor Neumann from a station on the middle Omo (BOULENGER, 1911).

The species was subsequently recorded from the actual lake by the 1930-31 Cambridge University Expedition (WORTHINGTON and RICARDO, 1936) and was encountered frequently during the present survey in collections from inshore sites.

Description: based on ten fish of 3.0-4.1 cm SL. Length 4.7-5.5 times the maximum depth and 3.8-4.1 times the length of the head. Diameter of eye 2.9-3.4 times in the length of the head, slightly greater than either the length of the snout or the interorbital width. Pectoral fin 0.77-0.85 times the length of the head, its tip falling well short of the pelvic fin origin. Dorsal fin originating slightly behind the mid point between the tip of the snout and the end of the caudal peduncle, the base almost entirely in front of the vertical to the origin of the anal fin. Dorsal fin rays III 8, anal fin rays III 9-11 (M=10). Lateral line scales 37-39 (M=39), 5½ scales between the lateral line and the origin of the dorsal fin. Scales round the caudal peduncle 12.

Colouration: Silvery with steely blue iridescence. In formalin-fixed specimens, body marked with a dark mid dorsal black line and a broader but more diffuse mid lateral stripe.

Diagnosis: easily distinguished from other cyprinid fish in the Lake Turkana basin by the rather oblique, lipless mouth combined with the centrally placed dorsal fin and the characteristic lateral line and fin ray counts.

Food: zooplankton and aquatic insects.

Breeding: non-anadromous. Breeds in marginal waters of the main lake. Matures at 3.5-4.0 cm FL.

Distribution: inshore species restricted to the margins of the lake within the 8 metre contour. Marked preference for stony and rocky shores. Most abundant in the southern basin of the lake.

Elsewhere widely distributed in the soudanian region from the Volta through the Niger and Chad basins to the Nile where it extends upstream as far as Lake Mobutu (formerly Lake Albert).

Commercial importance: nil

Maximum recorded size: in Lake Turkana 6 cm FL

Genus *Engraulicypris* Gunther, 1893

Small slender cyprinid fish, body strongly compressed, belly not keeled. Lateral line dips low below the horizontal myoseptum and runs parallel with the ventral outline of the body. Mouth large, oblique, lipless. Dorsal fin originating in the posterior half of the body close to the vertical to the origin of the anal fin.

Engraulicypris stellae Worthington, 1932

(Fig. 5.30)

Engraulicypris stellae, a species endemic to Lake Turkana, was first collected by the 1930-31 Cambridge University Expedition. During the present investigations this small fish proved to be common and often abundant in all parts of the lake.

Description : based on adult fish of 2.5-2.9 cm SL. Length 4.7-5.3 times the maximum depth and 4.0-4.4 times the length of the head. Dorsal fin rays II 7-9. Anal fin rays III 12-17, most usually III

13-15 (M=III 14). Lateral line scales 34-37. Scales between lateral line and the origin of the dorsal fin 4½-5½.

Colouration: Silvery. In formalin-fixed specimens the body is marked with a broad, intensely black mid-lateral line.

Diagnosis: distinguished from Chelaethiops bibie, which it closely resembles, by its lower lateral line and anal fin ray counts, combined with relatively short pectoral fins, a curved pre-dorsal profile, the broad black mid-lateral band and the lack of a line of pigment at the base of the anal fin.

BOULENGER (1911) recorded E. bottegi (Vinc.) from Lake Turkana and from the River Omo but no subsequent specimens have been obtained. WORTHINGTON and RICARDO (1936) thought it likely that the Lake Turkana record was the result of a misidentification of E. stellae. Engraulicypris bottegi differs from E. stellae in having 40-45 lateral line scales and 15-17 branched anal fin rays.

Food: chiefly zooplankton (see page 1513).

Breeding: spawns within the lake. Matures at ca 2.2 cm FL

Distribution: endemic to Lake Turkana. Widely distributed both in inshore and in offshore waters where, as a pelagic species, it extends throughout the water column into the deepest parts of the lake. At times abundant.

Commercial importance: no direct value but an important link in the food chains of several valuable commercial species of fish.

Maximum recorded size: 3.3 cm FL

Genus Chelaethiops Boulenger, 1899

A genus erected for small cyprinid fish similar to Engraulicypris but with the body keeled between the pectoral fins. No keel was, however, discernable in any Chelaethiops examined during the course of the present studies in the British Museum (Natural History).

Chelaethiops bibie Joannis, 1839

(Fig. 5.31)

Previously unknown in the Turkana basin, C. bibie was encountered frequently in more northerly parts of Lake Turkana during the present investigations.

Description: based on 10 fish of 2.8-3.5 cm SL. Length 4.4-5.2 times the maximum depth and 4.0-4.3 times the length of the head. Axis of head tilted slightly upwards to the front relative to the body, so that the downward curve of the predorsal profile is interrupted at the junction of head and body. Diameter of eye 3.04-3.44 times in the length of the head, usually slightly greater than either the length of the snout or the interorbital width. Pectoral fin long, 1.14-1.27 times the length of the head, its tip easily overlapping the base of the pelvic fin. Body between pectoral fins not keeled. Dorsal fin short, 0.54-0.59 times the length of the head, its origin lying posterior to the vertical to the origin of the anal fin. Dorsal fin rays III 7, rarely III 6 or III 8. Anal fin rays III 14-18 (M=16-17). Lateral line scales 36-42 (M=39-40). Scales between the lateral line and the origin of the dorsal fin 5½, rarely 6½. Scales round caudal peduncle 12.

Colouration: silvery, tinged with yellow on the dorsal surface. Lower lobe of caudal fin and the base of the anal fin clear yellow. In formalin-fixed specimens horizontaal myoseptum a slender black line bordered dorsally by a broad but diffuse band of melanophores. A line of dark spots at the base of the anal fin is conspicuous in smaller fish but tends to become faint in larger individuals.

Diagnosis: considered under *E. stellae* above.

Food: chiefly zooplankton and aquatic insects (see page 1514).

Breeding: probably spawns within the lake. Post larvae widespread in the open waters of the northern basin during the flood season. Matures at 3.5-4.0 cm FL.

Distribution: chiefly inshore in distribution, commonest at the northern end of the lake. Absent from the southern basin.

Elsewhere widespread in the River Nile. Also recorded from the Webi Shebeli in Somalia.

Commercial importance: nil

Maximum recorded size: in Lake Turkana 5.1 cm FL

Family Bagridae

Genus *Bagrus* Cuvier, 1817

Body moderately elongated. Dorsal and anal fins short. Adipose fin large and elongated. Pectoral and dorsal fins each with a spine. Head bearing four pairs of barbels including a pair of long maxillary barbels extending posteriorly at least to the level of the pectoral fin. Teeth minute, villiform, massed together in pads or bands. Transverse tooth bands on both jaws, the premaxillary band with a second crescent-shaped band of vomeropterygoid teeth situated close to its rear.

Bagrus bayad Forsskål, 1885

(Fig. 5.32)

Turkana name: lorok

Bagrus bayad was first collected from Lake Turkana by the 1930-31 Cambridge University Expedition (WORTHINGTON and RICARDO, 1936). During the present survey the species proved to be the predominant demersal fish in the offshore waters of the lake. Details of a biological study are given on pages 1023 to 1043.

Description: based on 14 fish of 10.7-31.6 cm SL. Body elongated, length 5.2-6.6 times the maximum depth and 3.5-4.3 times the length of the head. Head somewhat depressed, 1.7-2.2 times as long as broad, dorsal surface sculptured with a series of irregular longitudinal ridges. Interorbital width 5.8-7.7% of the standard length. Maxillary barbel very long, 0.9-1.3 times (negative allometry) the standard length, the tip overlapping the caudal fin in all but the largest individuals. Branched dorsal fin rays 9-11 (M=10). Branched anal fin rays 8-10 (M=9). Tips of both upper and lower lobes of the caudal fin elongated to form fine filaments.

Colouration: pale grey or fawn, dirty white below. Fish trawled from deeper water often with reddish fins due to ruptured blood capillaries.

Diagnosis: more slender than *B. docmac* with a narrower head, less rounded snout and eyes set more closely together. The longitudinal striations on the dorsal surface of the head in the present species are lacking in *B. docmac* which has a smooth and slightly convex orbital region. *Bagrus bayad* also has a relatively longer maxillary barbel and both upper and lower lobes of the caudal fin bear filaments with only the upper lobe in *B. docmac*.

Food: principally fish and prawns (see page 1035).

Breeding: spawns within the main lake during the flood season. Matures at 35-40 cm FL (see page 1030)

Distribution: demersal species, common and ubiquitously distributed in deeper water below the 15 metre contour. More occasional in shallow water inshore (see page 1020)

Extends over much of the soudanian region from Senegal through the Volta, Niger and Chad basins to the Nile where it extends upstream as far as Lake Mobutu (formerly Lake Albert).

Commercial importance: a commercial species which has increased in importance since the introduction of gillnets in 1972. By 1974 the annual catch of *B. bayad* had risen to 262 tonnes wet weight, equivalent to 7.5% of the total catch.

Maximum recorded size: in Lake Turkana 90 cm FL

Bagrus docmac Forsskål, 1775

(Fig. 5.33)

Turkana name: lisi

Bagrus docmac was first obtained from the Turkana basin by Zaphiro and McMillan who collected a specimen from the Engino River, a tributary of the River Omo in 1908 (BOULENGER, 1911). The species was not subsequently recorded from the area until the present survey in the course of which small numbers were caught sporadically in the main lake.

Description: based on 12 fish of 9.2-29.5 cm SL with additional data on an individual of 79 cm SL. Length 4.2-5.5 times the maximum depth and 3.2-4.0 times the length of the head. Head 1.1-1.5 times as long as broad, dorsal surface smooth. Interorbital width 8.4-10.7% of the standard length. Maxillary barbel 0.65-0.95 times the standard length, negatively allometric and only 0.4 times the standard length in the fish of 79 cm SL. Tip of maxillary barbel reaching the anal fin in the smallest individuals. Branched dorsal fin rays 9. Branched anal fin rays 8-9. Tip of the upper lobe of the caudal fin elongated to form a filament.

Colouration: usually dark grey or brown above, but black in specimens caught in clear shallow water in the southern basin. Whitish below.

Food: chiefly fish (see page 1044).

Distribution: demersal fish, generally scarce. Mostly recorded from rocky substrates in water of moderate depth offshore but a few specimens caught by rod and line on rocky coastlines.

Elsewhere widespread in the soudanian region from the Volta through the Niger and Chad basins to the Nile system where it occurs upriver as far as Lake Victoria. Also recorded from the basins of Lake Stephanie and Lake Abaya.

Commercial importance: a valuable commercial species but of little importance in Lake Turkana due to its comparative rarity.

Maximum recorded size: in Lake Turkana 110 cm.

Genus Chrysichthys Bleeker, 1858

Body moderately elongated, slightly compressed. Dorsal, adipose and anal fins short. Pectoral and dorsal fins with spines. Four pairs of barbels, the maxillary barbels of moderate length. Teeth minute, villiform, arranged in pads or bands. Transverse tooth bands on both jaws, the premaxillary band narrowly separated from a crescentic band of vomeropterygoid teeth.

Chrysichthys auratus Geoffroy Saint-Hilaire, 1809

(Fig. 5.34)

Chrysichthys auratus was previously unrecorded from the Turkana basin. During the present survey this small species of catfish proved to be plentiful, and at times abundant in Lake Turkana. An account of the biology of C. auratus is given on pages 1045 & 1046).

Description: based on 25 fish ranging from 7.2 to 11.5 cm SL. Length 4.1-5.1 times as long as deep and 3.2-3.8 times the length of the head. Head 1.3-1.6 times as long as broad. Eyes large, oval, dorso-lateral and prominent, the maximum diameter 2.3-3.4 times in the length of the head. Snout viewed from above tapering to a blunt point, its length 0.7-1.1 times the diameter of the eye. The profile of the head falls steeply in front of the eye. Maxillary barbel approximately the same length as the head, its tip just overlapping the base of the pectoral fin. Dorsal fin rays I 6, the first soft ray slightly elongated to form a short filament. Branched anal fin rays 7-8. Spine of pectoral fin curved, with strong serrae on the inner edge. Caudal fin deeply forked, the upper lobe slightly longer and more pointed than the lower but not produced to form a distinct filament.

Colouration: fawny-brown above with silvery iridescence on the flanks, whitish below. Distal margin of dorsal fin narrowly edged with black. Black edging to dorsal and distal margins of caudal fin.

Diagnosis: easily separated from Auchenoglanis by a number of diagnostic characters including the deeply cleft caudal fin and the small adipose fin. The dentition is similar to Bagrus from which Chrysichthys may be distinguished by the relatively short maxillary barbel, small adipose fins and the characteristic fin ray counts.

Food: chiefly prawns and small fish (see page 1046).

Breeding: spawns within the confines of the main lake. Matures at 7-8 cm FL (see page 1046).

Distribution: usually demersal, occurring both inshore and offshore, particularly between the 10 and 20 m contours where at times abundant.

Elsewhere widely distributed in the soudanian region from the Volta, through the Niger and Chad basins to the Nile. Apparently does not extend up the Nile as far as the Ugandan frontier.

Commercial importance: not at present caught in commercial nets and due to small size, not likely to be of economic importance.

Maximum recorded size: in Lake Turkana 30 cm FL.

Genus Auchenoglanis Gunther, 1865

Body moderately elongated, slightly compressed. Dorsal and anal fins short. Adipose fin long. Pectoral and dorsal fins each with a spine.Three pairs of barbels, maxillary and two pairs of mandibular Jaws with minute villiform teeth arranged compactly in rounded pads. Palate toothless.

Auchenoglanis occidentalis Cuvier and Valenciennes, 1840

(Fig. 5.35)

Recorded from Lake Turkana by BOULENGER (1911) but not observed by subsequent workers until MANN (1964) collected specimens in the Ferguson's Gulf aarea. During the present study, the species proved to be extremely rare in the lake and only one individual of 24 cm TL was caught.

Description: Length 3.5-5 times the maximum depth and 2.6-3.3 times the length of the head. Anterior end of fish wedge shaped in profile. Snout rather pointed in dorsal aspect, very long, usually more than half the length of the head and 3 (in young) to 8 times the diameter of the eye. Lips papillose, loose and membraneous. Maxillary barbel a little shorter than the outer mandibular barbel, not extending beyond the posterior border of the eye. Dorsal fin rays I 7. Branched anal fin rays 6 or 7. Pectoral spine strongly serrate on inner edge. Adipose fin large with the posterior border extending backwards as a lobe. Caudal fin with distal margin straight or slightly emarginate.

Colouration: olive or yellowish brown, uniform or with large dark brown or blackish spots on both body and fins.

Diagnosis: see C. auratus above.

Distribution: the range of A. occidentalis in Lake Turkana seems to have contracted since 1963 when MANN (op. cit.) encountered the species at Ferguson's Gulf. The single fish recorded during the present survey was caught in the north east corner of the lake within the overall region of the Omo delta. It seems likely that the species is nowadays principally riverine in distribution and that only occasional stragglers penetrate downstream to the northern fringe of the lake.

Elsewhere A. occidentalis is widely distributed occurring through most of the soudanian region from Gambia to the Lower Nile. The species also occurs in Lakes Tanganyika, Mweru and Bangwelu and in the Congo basin.

Maximum recorded size: attains a length of up to 51 cm TL.

Family Schilbeidae

Genus Schilbe Cuvier, 1817

Body elongated, strongly compressed. Dorsal fin short with 5-6 branched rays and a spine serrated on the posterior edge. Pectoral spine present, serrated in inner edge. Anal fin very long with more than 50 rays. No adipose fin. Four pairs of barbels present. Jaws with minute villiform teeth. Vomero-palatine tooth band also present.

Schilbe uranoscopus Rüppel, 1832

(Fig. 5.36)

Turkana name: naili

First recorded from Lake Turkana by WORTHINGTON (1932) who drew attention to the intermediate form of the population, with certain characters resembling S. uranoscopus and others S. mystus (L). He noted that the Lake Turkana fish resembled S. uranoscopus in the shape of the head and the short maxillary barbel and S. mystus in the relatively low number of anal fin rays. The Turkana specimens were considered to fall in between the two species in the shape of the predorsal profile and eye size. Although the anal fin ray count of 63-67 in Worthington's material lies within the range of 53-67 for S. mystus quoted by BOULENGER (1911), the modal number for the latter species is usually well below 60. During the present investigations a range of 61-70 anal fin rays with a mean of 64.8 was recorded for the Lake Turkana population which overlaps with the range of 67-75 for S. uranoscopus for the Nile. Thus the anal fin ray number is also an intermediate character and in most respects the Turkana fish are closer to S. uranoscopus. There is no reason to alter Worthington's original diagnosis.

Schilbe uranoscopus was caught commonly during the present survey and a detailed study has been carried out on its biology (see page 1048).

Description: based on 5 fish of 15.2-16.6 cm SL with counts and measurements on a further 18 fish. Length 4.0-4.9 times the maximum depth and 4.7-5.1 times the length of the head. Head 1.5-1.8 times as long as broad. Eye 4.0-4.5 times in the length of the head and 1.5-1.9 times in the interorbital width. Predorsal profile noticeably humped, falling steeply from the dorsal fin and levelling out on the head. Anal fin rays 61-70.

Colouration: mainly silvery, with steely-blue sheen on the dorsal surface, whitish below. Caudal fin with a dark streak on the upper lobe, particularly noticeable in juvenile fish.

Diagnosis: the combination of the very long anal fin, the short dorsal fin set well forward, the presence of spines on the dorsal and pectoral fins and the lack of an adipose fin distinguish S. uranoscopus from other catfish which occur or might occur in the Turkana basin.

Food: small fish and prawns (see page 1056).

Breeding: anadromous, migrating into the major rivers to spawn during the flood season. Matures at 16-19 cm FL (see page 1055).

Distribution: mainly pelagic in distribution, locally common in the open waters of the lake at depths of 10-25 metres. Also occurs regularly but in small numbers in shallow water inshore. Elsewhere restricted to the Nile basin.

Commercial importance: not at present fished commercially but an edible species and potentially of minor importance in an offshore gillnet fishery using nets of 2-3 inch mesh.

Maximum recorded size: in Lake Turkana 34 cm FL

Family Amphiliidae

Genus Andersonia Boulenger, 1900

Body elongated, depressed, with long and slender caudal peduncle. Series of overlapping bony scutes run along each side of the back and belly from the dorsal and pelvic fins to the tip of the caudal peduncle, which is completely encased. Two short dorsal fins present, the posterior, corresponding to the adipose fin in most siluriform fish, is also rayed. Mouth small, inferior, with numerous small conical teeth restricted to the premaxillary. Two pairs of mandibular and a pair of maxillary barbels present.

Andersonia leptura Boulenger, 1900

(Fig. 5.37)

Recorded by PELLEGRIN (1935) in the collection of fish from the Omo delta made by the 1932-33 Mission Scientifique de l'Omo. No subsequent specimens have been recorded.

Diagnosis: this aberrant species, with the body 9-10 times as long as the maximum depth, should be easily recognisable from the generic characters given above.

Distribution: the Turkana basin known only from two individuals of 2.3-2.8 cm TL collected from the Omo delta. Elsewhere recorded from the Nile and Chad basins.

Commercial importance: nil

Family Clariidae

Genus Clarias Scopoli, 1777

Body elongated with long dorsal and anal fins consisting entirely of soft rays. Head much flattened with heavy covering of dermal bones on the dorsal and lateral surfaces. Four pairs of barbels present. Jaws with well developed bands of closely packed villiform teeth. A band, often crescentic, of granular or villiform teeth on the vomer. Accessory breathing organs present in a pair of suprabranchial chambers consisting of dendritic outgrowths from the dorsal extremities of the gill arches.

Clarias lazera Cuvier and Valenciennes, 1840

(Fig. 5.38)

Turkana name: kopito

Clarias lazera was first collected from the Turkana basin in the Ferguson's Gulf area by the 1930-31 Cambridge University Expedition (WORTHINGTON and RICARDO, 1936). The species was caught in relatively small numbers during the present survey. A brief account of its biology is given on pages 1046 to 1047.

Description: length 5-9 times the maximum depth and 3.0-3.5 times the length of the head. Head 1.5-1.7 times as long as broad, the dorsal surface patterned with coarse granulations. Eye small.

Maxillary barbel approximately the same length as the head. Dorsal fin rays 62-82. Anal fin rays 50-65. Caudal fin rounded.

Colouration: usually olive brown but blackish in fish from clear shallow water. Whitish or greyish white below with a distinct black longitudinal band on either side of the ventral surface of the head.

Diagnosis: easily distinguished from Heterobranchus longifilis by the absence of an adipose fin.

Food: varied, chiefly zooplankton with smaller proportion of insects and fish (see page 1047).

Breeding: spawns during the flood season in the mouths of both major and ephemeral rivers. Matures at 65-70 cm TL (see page 1047).

Distribution: an inshore species caught in small numbers and restricted to shallow water within the 5 metre contour on both soft and hard substrates including rocky coastlines. Prefers sheltered situations. Crater Lake A on Central Island supports an isolated population.

Elsewhere very widely distributed including the whole of the soudanian region from Senegal to the Nile where it extends upstream as far as Lake Mobutu (formerly Lake Albert). Also occurs in Syria, Lake Galilee, Algeria, the basin of Lake Abaya and the Congo basin.

Commercial importance: a highly esteemed fish but of relatively minor importance in Lake Turkana due to comparative scarcity. During 1974 commercial catches of C. lazera amounted to 42 tonnes wet weight, 1.2% of the total output of the lake.

Maximum recorded size: in Lake Turkana 110 cm TL

Genus Heterobranchus Geoffroy Saint-Hilaire, 1809

Similar to Clarias (see above) but distinguished by the presence of a large adipose fin.

Heterobranchus longifilis Cuvier and Valenciennes, 1840

(Fig. 5.39)

Turkana name: labé

Collected from two tributaries of the middle Omo by Zaphiro and McMillan in 1908 (BOULENGER, 1911). No further specimens have been reported by subsequent investigators and the species was not handled during the present survey. However, a fish called labé is well known to Turkana fishermen in the region of the Omo della and was recorded in small quantities at the Todenyang co-operative under this name. Unfortunately no recognisable specimen was ever produced for critical examination but from the descriptions supplied by fishermen it is clear that a species of Heterobranchus is involved. Since H. longifilis is already known from the basin it seems highly probable that this is the species occurring in the Omo delta.

Diagnosis: easily distinguished from Clarias lazera by the presence of an adipose fin which is approximately the same length as the rayed dorsal fin. Maxillary barbels much longer than in C. lazera extending to beyond the tip of the pectoral fin.

Distribution: in the Turkana basin probably restricted to the River Omo and its delta.

Elsewhere widely distributed throughout the soudanian region from Senegal through the Volta, Niger and Chad basins to the Nile. Also occurs in the Congo and Zambezi systems where it has become established in Lake Kariba.

Commercial importance: during 1973 the equivalent of 1.2 tonnes wet weight of *H. longifilis* was marketed at the Todenyang co-operative.

Maximum recorded size: specimens up to 117 cm TL have been recorded in Lake Kariba (FRANK, 1974).

Family Malapteruridae

Genus *Malapterurus* Lacepède, 1803

Body moderately elongated, cylindrical. Rayed dorsal fin absent but a comparatively small adipose fin situated close to the caudal fin is present. Pectoral fin with a spine. Anal fin with 6 rays. Maxillary and two pairs of mandibular barbels present. Jaws with bands of villiform teeth but palate toothless. The body is enclosed within an electric organ which forms a thick, firm but elastic gelatinous sheath over the entire surface.

Malapterurus electricus Gmelin, 1782

(Fig. 5.40)

Turkana name: lasali

First recorded from the Turkana basin by PELLEGRIN (1935) who examined a specimen caught in the Omo delta by the 1932-33 Mission Scientifique de l'Omo. None was noted by subsequent investigators but during the present study two fish of 20 cm and 30 cm TL were caught in the Central and Turkwell Sectors of Lake Turkana at a considerable distance from the River Omo.

Diagnosis: the generic description above provides sufficient details for the identification of this species which is easily distinguished from other catfish in Lake Turkana by the form of the cylindrical body with its enveloping electical sheath. The disposition of the fins is also diagnostic.

Colouration: greyish or pinkish white with irregular black blotches more concentrated near the posterior end of the body.

Distribution: an uncommon species in the Turkana basin but widespread, occurring both in lacustrine and riverine environments. It is reliably reported (J. Rienks, pers. comm.) that *M. electricus* is also present in the River Turkwell system at Mamatte.

Elsewhere, widely distributed in tropical Africa, including the entire soudanian region, many minor coastal rivers in West Africa, the Ogowe and Congo basins and Lake Tanganyika.

Family Mochokidae

Genus Synodontis Cuvier, 1817

Body short or moderately elongate, slightly compressed. Dorsal fin short with 6-7 branched rays. Adipose fin large. Strong spines on dorsal and pectoral fins. Dermal bones forming heavy shield over dorsal and lateral surface of head, extending along the back to the dorsal fin and fused to the pectoral girdle. Three pairs of barbels, the inner and outer mandibular barbels always branched, the maxillary barbels usually simple. Premaxillary teeth conical, arranged in transverse series. Mandibular teeth 6-90, implanted in the lower lip, variable in form, with cusps or entire. Palatine teeth absent.

Synodontis schall Bloch-Schneider, 1801

(Fig. 5.41)

Turkana name: tirr

Synodontis schall was first collected in the Turkana basin in 1908 by Zaphiro and McMillan (BOULENGER, 1911). The species was found to be common in Lake Turkana by subsequent workers and during the present investigations heavy concentrations were at times encountered. A detailed biological study is present on pages 1059 to 1081.

Description: based on 11 fish of 14.7-26.2 cm SL from the Ferguson's Gulf area. Length 3.3-4.3 times the maximum depth and 3.18-3.77 times the length of the head. Head 1.2-1.6 times as long as broad. Eye 4.9-5.7 times in the length of the head and 1.6-2.2 times in the interorbital width. Pectoral spine 0.85-1.05 times as long as the head, finely serrated on outer edge, strongly serrated on inner edge. Dorsal fin rays I 7, the spine similar in length to the pectoral spine, minute denticulations on anterior edge, weakly serrated behind. Maxillary barbel lacking obvious membrane, 1.1-1.3 times the length of the head. Outer mandibular barbel 0.6-0.8 times the length of the maxillary with long slender branches. Inner mandibular barbel approximately half the length of the outer with slender branches the more basal of which bear short tubercular outgrowths at their bases. Premaxillary teeth in a band less than the diameter of the eye in width. Mandibular teeth 23-33.

Colouration: olive brown or greyish above, dirty white below. The body is often peppered with fine black spots particularly noticeable in juvenile fish. Specimens from clear shallow water in the south of the lake are sometimes entirely black in colour.

Diagnosis: similar to S. frontosus Vaill., the only other species of Synodontis so far recorded from the Turkana basin. The two species differ in the following respects:

S. schall	S. frontosus
Interorbital region narrower; orbits lie well within the lateral margin of the head when viewed from above	Interorbital region broader; orbits impinge on the lateral outline of the head when viewed from above
Snout rather pointed	Snout more broadly rounded
23-33 mandibular teeth	36-48 mandibular teeth

S. schall	S. frontosus
Base of maxillary barbel with no membrane on inner margin	Maxillary barbel with narrow but conspicuous black membrane on inner margin for at least basal third of length
Width of premaxillary tooth band less than diameter of eye	Width of premaxillary tooth band greater than diameter of eye
Humeral process with striated surface sculpturing	Humeral process with granular surface sculpturing
Pectoral spine with fine but sharp and obvious serrations on anterior edge	Pectoral spine with barely discernable serrations on anterior edge

Food: very variable including zooplankton, insects, molluscs, prawns and small fish (see page 1076).

Breeding: spawns in the mouths of both major and ephemeral rivers during times of spate. Matures at 19-21 cm FL (see page 1068).

Distribution: widespread and numerous in all areas of the lake, both inshore and offshore. Often swims freely as a pelagic fish in the midwater and surface layers of the open lake. At times abundant in the Central and Northern Sectors of the lake between the 10 and 20 metre contour. An isolated population inhabits Crater Lake A on Central Island.

Elsewhere widely distributed throughout the soudanian region from Senegal, through the Volta, Niger and Chad basins to the Nile where it extends upstream as far as Lake Mobutu (formerly Lake Albert). Populations of S. schall also occur to the north east of Lake Turkana in Lake Abaya and the Webi Shebeli system.

Commercial importance: a valuable species forming a high proportion of the fish removed by the Turkana fishermen from the catch for local consumption. The total catch of S. schall rose from 83 tonnes wet weight in 1972 to 262 tonnes in 1974.

Maximum recorded size: in Lake Turkana 35 cm FL

Synodontis frontosus Vaillant, 1895

(Fig. 5.42)

First collected from the Turkana basin at a station on the River Omo by Donaldson Smith in 1895 and subsequently obtained in the north east corner of the main lake by Zaphiro and McMillan in 1908 (BOULENGER, 1911). No specimens were obtained by the 1930-31 Cambridge University Expedition whose studies were centred on the Ferguson's Gulf area (WORTHINGTON and RICARDO, 1936) but MANN (1964) notes the presence of S. frontosus together with S. schall in the same area during 1963. During the present study S. frontosus was never found in the actual lake but specimens were caught on each of the two occasions when fishing was carried out on the River Omo jut north of the delta at Lochius and at Kaalom. It would appear that the range of S. frontosus has shrunk considerably since 1963, possibly as a result of hydrological changes. A similar situation was noted in the case of Auchenoglanis occidentalis (see above).

Description: morphometric data are available for only two S. frontosus of 17 and 18 cm SL collected from the River Omo at Nachui on 2/3/73. In most instances the proportions fall into the ranges quoted for S. schall above, with the following exceptions. Maximum depth 3.1 times in the standard length. Interorbital width 2.1-2.3 times the diameter of the eye. Maxillary barbel 1.5-1.6 times the length of the head. Other diagnostic characters for S. frontosus appear in the table of comparisons (see S. schall above).

Colouration: greyish brown, darker above, paler below particularly on the ventral surface of the head. Body with a peppering of fine black spots.

Distribution: at present confined to the River Omo and its delta but recorded by MANN (op. cit.) from the Ferguson's Gulf area in 1963.

Elsewhere recorded from the Chad basin and from the Nile where it occurs upstream as far as Lake Mobutu (formerly Lake Albert).

Maximum recorded size: attains a size of ca 30 cm FL

Genus Mochocus Joannis, 1835

Small fish with the body moderately elongated. Head armoured dorsally and laterally with cephalo-nuchal shield of dermal bones extending posteriorly to envelop the base of the dorsal spine. Second dorsal fin with rays in place of adipose fin normally found in siluriform fish. Mouth small, subterminal with small conical teeth in both jaws. Palate toothless. Three pairs of barbels, the inner and outer mandibular barbels branched, the maxillary barbels simple.

Mochocus niloticus Joannis, 1835

(Fig. 5.43)

Recorded from Lake Turkana by BOULENGER (1911). No specimens were noted by subsequent investigators in the area but a single individual of 3.3 cm FL was collected during the present survey on the lake shore at Todenyang in September 1972.

Description: body slender, 4.3-5.7 times as long as deep. Head depressed, approximately as broad as long, dorsal surface roughly ridged. Eyes dorso-laterl, 3.0-4.5 times in the length of the head. Anterior dorsal fin with 7-8 soft rays, the spine weakly serrated on the anterior margin. Pectoral spine with strong curved serrae on inner edge, more weakly serrated on outer edge.

Colouration: specimen from Lake Turkana generally pale, marbled and speckled with brown.

Diagnosis: the slender form combined with the second rayed dorsal fin replacing the adipose fin, conical teeth and branched mandibular barbels separate this species from related forms.

Distribution: a rare but easily overlooked species probably confined to the Omo River and occurring only as a straggler in adjacent areas of the main lake.

Elsewhere widespread in the soudangian region from the Niger through the Chad basin to the Nile.

Commercial importance: nil

Maximum recorded size: grows to ca 6.5 cm TL

Family Cyprinodontidae

Genus Aplocheilichthys Bleeker, 1863

Head and body covered with cycloid scales. Dorsal surface of head flattened. Mouth small, premaxillary protractile. Both jaws with a band of conical teeth, the outer larger than the inner. Lateral line absent. Pectoral fin situated relatively high on the flanks. Origin of dorsal fin behind the vertical to the first anal fin ray. Caudal fin rounded.

Aplocheilichthys rudolfianus Worthington, 1932

(Fig. 5.44)

This endemic form was originally described from type material collected by the Cambridge University Expedition in the Ferguson's Gulf area. The species was caught regularly in shore samples during the present survey.

Description: based on 10 fish of 2.4-2.9 cm SL. Length 4.2-4.8 times the maximum depth and 4.1-4.4 times the length of the head. Snout 0.45-0.52 times the diameter of the eye, mouth superior. Eye 2.4-2.8 times in the length of the head and 0.79-0.92 times in the interorbital width. Pectoral fin 0.71-0.78 times the length of the head. Dorsal fin with 8-9 rays, 0.62-0.71 times the length of the head. Anal fin rays 14-16 (M=15). Caudal peduncle 2.1-2.5 times as long as deep. Scales in longitudinal series 28-30 (M=29).

Colouration: body yellowish with a peppering of fine melanophores outlining the scales and heaviest on the dorsal surface. Dark pigment on the distal margin of the anal fin rays and on the anterior rays of the dorsal fin. Basal portion of anal, dorsal and pelvic fins suffused with lemon yellow.

Diagnosis: apart from a slight increase in the range of fin ray and scale numbers, the present observations tally closely with Worthington's original description which was based on four individuals. The present species is distinguished from A. jeanneli (Pellegrin) which was described from the Omo delta by the more slender body and higher numbers of longitudinal scales and anal fin rays (see below).

Food: zooplankton and insects

Breeding: breeds within the lake. Matures at 2.5 cm TL

Distribution: endemic to Lake Turkana. Restricted to the shallow margins of the lake in sheltered situations with macrophytic vegetation.

Maximum recorded size: 2.6 cm TL

Aplocheilichthys jeanneli Pellegin, 1935

An endemic species described from material collected by the 1932-33 Mission Scientifique de l'Omo from the Omo delta. No further specimens have been recorded and it is possible that the distribution of A. jeanneli does not extend downriver into the actual lake.

Diagnosis: distinguished from A. rudolfianus by the relatively deeper body which is 3.0-3.5 times as long as deep. There are 25-26 scales in the longitudinal series (cf 28-30 in A. rudolfianus) and 12-13 anal fin rays (cf 14-16 in A. rudolfianus).

Colouration: yellowish with each scale outlined in black. The body is marked with a blackish lateral band. Fins greyish.

Distribution: an endemic form at present known only from 4 specimens collected in the Omo delta.

Maximum recorded size: 2.6 cm TL

Family Centropomidae

Genus Lates Cuvier and Valenciennes, 1828

Body somewhat compressed covered with ctenoid scales which extend over the posterior surface of the head. Mouth large and protractile, the jaws with bands of villiform teeth forming rough-surfaced pads. Villiform teeth also situated in the roof of the mouth on the vomers, the palatines and the ectopterygoids. Head with small spines borne laterally on the orbital and preopercular bones and on the free edge of the operculum. Dorsal fin deeply divided into two, the anterior section containing 7-8 spines and the posterior section one spine and 8-11 branched rays. Anal fin rays III 6-9. Pelvic fin with a single spine.

Lates niloticus (L) 1762

(Fig. 5.45)

Turkana name: iji English name: nile perch

WORTHINGTON (1932) was first to report Lates from the Turkana basin. He found two distinct forms which he described as subspecies of L. niloticus, a large inshore form L. rudolfianus and a smaller offshore form L. n. longispinis. He commented on the similarity of this situation with Lake Albert where he had previously found and described L. albertianus (=L. niloticus) and L. macrophthalmus (WORTHINGTON, 1929). The material has been re-examined by GREENWOOD (1976) who concluded that L. n. rudolfianus must be regarded as a synonym of the nominate species. He proposed, however, that L. n. longispinis should be treated as a full species L. longispinis Worthington (1932) pending a closer study of its relationship with L. macrophthalmus, the small offshore species from Lake Albert. Both L. niloticus and L. longispinis were taken commonly during the present investigations.

In order to compare the morphometry of two species which differ so markedly in size (L. niloticus attains a maximum size of at least 196 cm TL, cf 44 cm in L. longispinis) the description which follows relates chiefly to immature L. niloticus of 19-35 cm SL augmented with observations on a few larger individuals.

Description: based on 43 fish of 19-35 cm SL with additional notes on 8 fish of 36-66 cm SL. Body 3.0-3.6 times as long as deep and 2.9-3.4 times the length of the head. Eye 3.6-5.6 times in the length of the head (negative allometry) and up to 7.1 times in the head length in the larger fish. Length of snout 0.9-1.3 times the diameter of the ye (up to 1.6 times in larger fish). Interorbital width 0.5-0.8 times the diameter of the eye (up to 1.1 in larger fish). Pectoral fin 0.44-0.59 times as long as the head. Dorsal fin with 9 spinous and 10-12 branched rays (M=11). Third dorsal spine 0.55-0.73 times as long as the head (as little as 0.44 times in larger fish). Anal fin rays III 8. Caudal peduncle 1.36-1.56 times as long as deep. Lateral line scales 67-81. Scales round caudal peduncle 28-34.

Colouration: juveniles with cryptic colour pattern consisting of dark brown patches on a dull yellow background. This livery is gradually lost between a length of 20 and 40 cm TL. Adults silvery or brassy, darker above, whitish below. A rare lutino form of L. niloticus occurs in Lake Turkana. Such 'golden perch' are most strikingly pigmented rich orange yellow both on the body and on the fins. The body has a golden iridescence.

Diagnosis: the distinctions between L. niloticus and L. longispinis are discussed in the description of the smaller species below.

Food: fish, chiefly cichlids and characins up to 50% of own body length (see page 1294).

Breeding: spawns within the main lake producing pelagic embryos. Breeding activity continues throughout the year. Males mature at 65-70 cm and females at 85-90 cm TL.

Distribution: juveniles up to 40 cm TL restricted to inshore waters. Larger fish range widely, extending throughout the open water of the lake but highest concentrations found in sheltered areas on the east coast within the 10 metre contour.

Elsewhere widely distributed throughout the soudanian region from Senegal to the Nile where the range has recently been extended by artificial introductions to include Lakes Kyoga and Victoria.

Commercial importance: a high quality fish with annual catches from Lake Turkana fluctuating between 400 and 500 tonnes wet weight over the last five years. Lates niloticus also provides the basis for sport fishing at three tourist lodges on the shores of the lake.

Maximum recorded size: in Lake Turkana 196 cm TL (114 kg).

Lates longispinis Worthing, 1932

Turkana name: iji

An endemic species originally described as a subspecies of L. niloticus but now considered by GREENWOOD (1976) to be a distinct species. Caught frequently, at times abundantly, during the present survey.

Description: based on 15 fish of 19-36 cm SL with additional information on 3 fish of 14-15 cm and 4 fish of 32-40 cm SL. Length 3.3-3.8 times the maximum depth and 3.1-3.4 times the length of the head. Eye diameter 4.0-5.0 times in the length of the head (negative allometry), 0.96-1.31 times in the length of the snout and 0.56-0.71 times in the interorbital width. Pectoral fin 0.58-0.68 times the length of the head. Dorsal fin with 9, rarely 8 spinous rays and 11, rarely 10 branched rays. Third dorsal spine 0.68-0.80 times as long as the head. The length of this spine shows positive allometry in fish up to ca 14 cm SL and negative allometry in larger individuals. In fish of ca 14 cm the length of the third dorsal spine may approach the length of the head. Anal fin rays III 8. Caudal peduncle 1.56-2.03 times as long as deep. Lateral line scales 63-76. Scales round caudal peduncle 28-34.

Colouration: silvery, greyish above, whitish below. A spot of black pigment at times present on the tip of the spinous dorsal between the 3rd and 4th rays.

Diagnosis: care is needed to separate the present species from L. niloticus. The proportions given in the following comparison apply to fish of ca 19-35 cm SL. Allowances should be made for allometry in fish outside this range or when comparing fish varying markedly in size.

Lates longispinis	Lates niloticus
More elongated and angular in appearance with lower condition factor	More compact and rounded in appearance with higher condition factor
Caudal peduncle slender, 1.56-2.03 times as long as deep	Caudal peduncle stout, 1.15-1.62 times as long as deep
Pectoral fin longer, 0.58-0.68 times length of the head	Pectoral fin shorter, 0.44-0.59 times length of the head
Third dorsal spine longer, 0.68-0.80 times length of head	Third dorsal spine shorter, 0.55-0.73 times length of head
Eye slightly larger	Eye slightly smaller
Matures at 25-30 cm TL	Matures at 65-90 cm TL
Ranges chiefly offshore beyond the 10 metre contour. Enters shallow water only at north end of lake when conditions turbid	Ranges inshore and offshore but fish of under 35 cm TL very rare below the 10 metre contour

Food: chiefly prawns and small characins (see page 1320).

Breeding: spawns within the lake. Eggs and embryos probably pelagic. Matures at 25-30 cm FL (see page 1317).

Distribution: endemic to Lake Turkana. Ranges throughout the offshore waters of the lake chiefly beyond the 10 metre contour. A pelagic species forming part of the midwater community. Population densities vary considerably from area to area. Tends to concentrate near the west coast in more northerly areas of the lake.

Commercial importance: at present not fished commercially but of good quality though small in size. Difficult to catch in quantity with gillnets although catches up to 34.1 kg/hr taken in bottom trawls.

Family Cichlidae

Genus Hemichromis Peters, 1857

Body 2-3 times as long as deep. Scales cycloid or feebly denticulate. Two incomplete lateral lines. Jaws with one, rarely two rows of conical teeth. Dorsal fin with 13-15 spines. Anal fin with 3-4 spines.

Hemichromis bimaculatus Gill, 1862

(Fig. 5.46)

The 1930-31 Cambridge University Expedition collected three small cichlids from Lake Turkana which were described as a new species Pelmatochromis exsul Trewavas (1933). Recently it has been shown (TREWAVAS, 1973) that the specimens were misidentified and that they were in fact examples of H. bimaculatus, a widely distributed taxon. This species appears to be extremely scarce in Lake Turkana and in spite of an extensive shore survey which included all areas of the lake, only two individuals were caught during the present investigations.

Diagnosis: readily distinguished from other cichlids in Lake Turkana by the conical form of the teeth which are usually arranged in two rows, an outer row of relatively large teeth and a short row of minute inner teeth. Rarely, a third row of minute teeth is situated behind the second. Also distinguished from Haplochromis spp by the scales which are cycloid instead of ctenoid. Dorsal fin rays XIII-XV 9-13, anal fin rays III-IV 7-9. There are 25-29 scales in the longitudinal series, 15-19 in the upper lateral line and 7-11 in the lower.

Colouration: adult fish are brownish, marked with three conspicuous black lateral spots. Breeding fish become reddish and develop rows of small brilliant blue spots on the body and on the unpaired fins. Juveniles are striped with dark mid-dorsal and mid-lateral bands.

Food: in Lake Chad the food consisted chiefly of insects and small fish.

Breeding: an inshore species preferring inshore sites with vegetation cover. Rare in Lake Turkana and only 5 individuals recorded from the following sites: Allia Bay, Moite, El Molo Bay and Central Island.

Elsewhere widely distributed throughout the soudanian region from the Gambia to the Nile where it extends upstream to the region of Juba. Also recorded from many of the West African coastal rivers, from the Congo basin and from the Algerian Sahara.

Maximum recorded size: grows up to 15 cm TL

Genus Tilapia Smith, 1840

Body moderately deep. Scales cycloid or ctenoid. Two incomplete lateral lines. Teeth in two or more rows, the outer bicuspid (rarely conical), the inner rows tricuspid. Gillrakers on lower part of first branchial arch 7-16, rarely more than 12. Dorsal spines 11-19. Anal spines 3-4. Substrate spawners and brood guarders.

Tilapia zillii Gervais, 1848

(Fig. 5.47)

Turkana name: kokine

Tilapia zillii was first collected from Lake Turkana in 1895 (BOULENGER, 1915). The species was caught regularly in small numbers by subsequent investigators. During the present survey T. zillii proved to be more localised and far less abundant than Sarotherodon niloticus which was always the dominant cichlid of the inshore fisheries of Lake Turkana.

Description: body compressed, 2.1-2.7 times as long and 2.6-3.3 times the length of the head. Predorsal profile convex, relatively steep. Eye 3.5 (young)-5.0 times in the length of the head. Mouth large. Teeth in 3-6 rows. Number of teeth increasing with size of fish, 20-60 in the outer row of upper jaw. Gillrakers stout, 8-12 on lower part of first gill arch. Dorsal fin rays XIV-XVI 10-13. Anal fin rays III 7-10. Distal margin of caudal fin straight or slightly convex, distal corners of the fin rounded. Longitudinal series of scales 28-33. Three to four rows of scales on the cheek.

Colouration: scales generally greyish with pale iridescent green centres more brightly coloured on the dorsal surface than on the flanks. Ventral surface whitish. Body marked with 6 or 7 dark vertical bars of varying intensity, usually more pronounced in juveniles. Operculum with small iridescent green spots. Dorsal, anal and caudal fins greyish green with yellowish spots forming a reticulated pattern. Basal part of anterior soft dorsal rays with a distinctive black 'Tilapia' spot, persisting in adult fish.

Diagnosis: superficially similar to Sarotherodon niloticus and S. galilaeus but differs in head shape which is less symmetrical viewed laterally due to a steeper and more convex predorsal profile. Differences in colouration are also apparent but the most valuable diagnostic character is the low number of gillrakers on the lower part of the anterior arch (8-12 cf of over 20 in the two species of Sarotherodon).

Food: principally attached algal communities growing on rocks, sand or macrophytes. Small invertebrates living within the algal mats are also ingested and assimilated (see page 1365).

Breeding: substrate spawners breeding inshore within the main lake. Mature fish as small as 8 cm TL were recorded during the present studies (see page 1344).

Distribution: an inshore species usually confined to depths of less than 5 metres although once trawled from a depth of 16 metres on a submerged reef. Shows a clear preference for rocky substrates where usually plentiful. Common on the precipitous coastline of the southern basin. Generally scarce on finer substrates.

Elsewhere widespread throughout most of the soudanian region from the Niger basin through the Volta and Chad systems to the Nile. Recently introduced into Lake Victoria. Also occurs in Lake Galilee, in the Algerian Sahara and in certain coastal rivers of West Africa.

Commercial importance: a valuable commercial species which in Lake Turkana contributes only slightly to the commercial catch. With the population concentrated chiefly on inaccessible rocky coastlines it is unlikely that the yield will increase appreciably in the future.

Maximum recorded size: in Lake Turkana 33 cm TL

Genus Sarotherodon Rüppell, 1853

Closely resembling Tilapia. Differing chiefly in certain features of cranial osteology, in the presence of 10-28 gillrakers (rarely less than 13) and in the breeding habits. Sarotherodon spp are mouthbrooders.

Sarotherodon niloticus (L) 1757
(=*Tilapia nilotica*) (L)

(Fig. 5.48)

Turkana name: kokine

The species was first collected from Lake Turkana by Zaphiro and McMillan in 1908 (BOULENGER, 1915). Specimens were caught abundantly by the 1930-31 Cambridge University Expedition particularly in the Ferguson's Gulf area (WORTHINGTON and RICARDO, 1936). The material included examples of an isolated population from Crater Lake A, Central Island, which was described as a new species *Tilapia vulcani* Trewavas 1933. Dr Trewavas (pers. comm.) now regards the differences between *T. vulcani* and *S. niloticus* as ecophenotypic and *T. vulcani* is thus synonymised with *S. niloticus*. During the present investigations the species proved to be a common inshore form, at times very abundant. Details of biological investigations are given on pages to .

Description: body compressed, 2.0-2.6 times as long as the maximum depth and 2.6-3.3 times the length of the head. Predorsal profile straight or slightly convex. Eye 3.5 (young) to 5.7 times in the length of the head. Mouth moderate in size. Teeth in 2-7 rows with 30-90 in the outer row of the upper jaw, the number increasing with size. Gillrakers slender, 22-28 on the lower part of the anterior gill arch. Dorsal fin rays XVI-XVII (rarely XV or XVIII) 11-15. Anal fin rays III 8-11. Distal margin of caudal fin straight or noticeably convex, posterior corners of the fin rounded. Longitudinal series of scales 31-35. Two 3-rows of scales on the cheek.

Colouration: very variable. Body and flanks greyish or greyish green with dark patches on each scale giving a regular mottled appearance. Eight or nine narrow vertical black bars on the body usually present, particularly in juvenile fish. In large specimens from clear water in the southern basin, the pigmentation is often heavy and in some cases the entire fish is an almost uniform greenish black. Soft dorsal and anal fins chequered with alternate light and dark spots. Dark spots on the caudal fin are aligned to form a characteristic series of vertical stripes. The alignment tends to break up in adult fish, giving rise to a more random pattern. The black '*Tilapia*' spot is present only in juvenile fish.

Diagnosis: for characters separating *S. niloticus* and *S. galilaeus* and *T. zillii* refer to the accounts of these two species.

Food: successfully filters and assimilates a variety of blue-green algae which form its chief source of food in areas with dense phytoplankton concentrations, such as Ferguson's Gulf. Also grazes on algal populations growing on mud and sand surfaces, rocks etc.

Breeding: a mouth brooder. Spawns in sheltered inshore areas of the lake. The young are carried by the females. Usually in Lake Turkana *S. niloticus* matures at ca 32 cm TL but isolated populations in the vicinity of the lake show considerable reduction in the size of breeding adults. Thus in the springs at Loiengalani mature *S. niloticus* of 10-12 cm were observed.

Elsewhere very widely distributed, ranging over the entire soudanian region from Senegal to the Nile where it extends upriver as far as Lakes Edward and George. Also occurs in Lakes Galilee, Tana, Abaya, Baringo, Kivu and Tanganyika, the Awash, Wabi Shelebi and Ewaso Nyiro Rivers and the basin of the upper Congo. Recently introduced into Lakes Kyoga and Victoria.

Commercial importance: during the last 3 years has risen dramatically in importance to become the most valuable species in the Lake Turkana fishery. In 1976 a staggering 16000 tonnes was recorded, virtually the whole catch derived from a relatively tiny area of 10-15 km^2 in Ferguson's Gulf. There is strong evidence to show that the high yield was due to particularly favourable climatic conditions combined with other environmental factors (see page 1349).

Maximum recorded size: in Lake Turkana 64 cm TL

Sarotherodon galilaeus (Artedi), 1757

(= Tilapia galilaea (Art.)

(Fig. 5.49)

Turkana name: kokine

Sarotherodon galilaeus was first collected from Lake Turkana by the 1930-31 Cambridge University Expedition (WORTHINGTON and RICARDO, 1936). It was noted that out of large catches of cichlids only six of the present species were obtained. During the present investigations a similar dearth of S. galilaeus was evident, except in a few localised areas.

Description: body somewhat compressed and deep, 1.8-2.5 times as long as the maximum depth and 2.6-3.0 times the length of the head. Predorsal profile straight or slightly convex. Eye 3 (young)-6 times in the length of the head. Mouth small. Teeth in 3-10 rows with 40-120 in the outer row of the upper jaw. The number of teeth and tooth rows tends to increase with size. Gillrakers fine, 21-26 on the lower part of the first gill arch. Dorsal fin rays XVI-XVII (rarely XV) 12-14. Anal fin rays III 9-12. Distal margin of caudal fin straight or slightly emarginate, the posterior corners of the fin sharply angular. Longitudinal series of scales 28-31. Cheek with 2-3 rows of scales.

Colouration: body silvery, greyish above, whitish below. Flanks often marked with 3-5 dark, slender vertical stripes particularly noticeable in juvenile fish. Caudal fin unspotted with the distal margin broadly tipped with pale pink merging into grey on more basal parts.

Diagnosis: easily distinguished from both S. niloticus and T. zillii by the deep, more compressed body, by the emarginate, angular and unspotted caudal fin and by the predominantly silvery body lacking heavy mottling. Also separated from T. zillii by the high number of gillrakers on the first anterior gill arch.

Food: grazes on a mixture of phytoplankton and ebibenthic algae, feeding predominantly by filtering on the mud-water interface (see page 1365).

Breeding: a mouth brooder, spawning in marginal areas of the lake. Brooding is undertaken by the females. Matures at a length of ca 28 cm TL (see page 1344).

Distribution: an inshore species restricted to shallow water within the 5 metre contour. Widespread over substrates of soft mud but only locally common. Chief centres of distribution in sheltered bays on the east shore of the lake.

Elsewhere distributed throughout the soudanian region from the Gambia to the Nile where it extends upriver as far as Lake Mobutu (formerly Lake Albert). Occurs in Lake Galilee, the type locality.

Commercial importance: a valuable species but of relatively minor importance in Lake Turkana where S. niloticus dominates catches of cichlid fish.

Maximum recorded size: in Lake Turkana 35 cm TL

Genus Haplochromis

A large and very variable cichlid genus with strongly ctenoid scales and teeth in two or three rows. The external row of teeth are usually either conical or bicuspid and the inner row or rows are generally tricuspid. Two incomplete lateral lines. Dorsal fin with 13-19 spines. Anal fin with 3-6 spines.

Haplochromis rudolfianus Trewavas, 1933

(Fig. 5.50)

A common inshore form, endemic to Lake Turkana and first collected by the 1930-31 Cambridge University Expedition. GREENWOOD (1974) has recently re-described the species using the type specimens together with additonal material obtained during the course of the present study.

Description: based on GREENWOOD (op. cit.) and covering a size range of 3.9-5.8 cm SL. Body 3.0-3.4 times as long as deep and 2.8-3.2 times the head length. Head 2.8-3.3 times the eye diameter, 3.0-3.2 times the snout length and 3.9-5.7 times the depth of the cheek. Caudal peduncle 1.2-1.7 times as long as deep. Lateral line scales 30-33. Six or 7 scales between the dorsal fin origin and the upper lateral line. Cheek with 3 (rarely 2 or 4) rows of scales. Dorsal fin rays XIV-XVI 9-11. Anal fin rays III 8-11. Outer row of teeth of both jaws chiefly bicuspid with few unicuspid or tricuspid teeth at the posterior end of the row. Inner teeth all tricuspid, 2-3 (rarely 4) rows in the upper jaw and 2-3 (rarely 1) rows in the lower jaw.

Colouration: adult males with greenish yellow ground colour, whitish on the chest. Flanks and caudal peduncle with 5-10 dark vertical bars. Scales with conspicuous iridescence, bluish posteriorly and yellowish anteriorly. Operculum marked with golden-yellow. Branchiostegal membrane pale yellow with black anterior area. Dorsal fin membrane dark yellow with scarlet lappets, the soft rays spotted with yellow and black. Anal fin yellow, speckled with red and black, bearing two or three golden yellow ocelli. Caudal fin yellowish green with red and black spots. Adult females are similarly but much less brightly coloured with more extensive areas of white on the ventral surface and with no black on the branchiostegal membrane.

Diagnosis: distinguished from other Haplochromis in Lake Turkana by the barred colour pattern. Easily separated from H. macconneli by the absence of hypertrophied laterosensory canals and pores on the head and by the dentition. From H. turkanae, with which it is probably closely related phyletically, H. rudolfianus is separated morphologically by having four rows of scales on the cheeks (3 cf. 4 or 5), smaller scales between the pectoral and pelvic fin insertions (6 or 7 cf. 9 or 10), a less deep cheek (3.9-5.7 times in the length of the head cf. 3.1-3.8 times) and shorter upper and lower jaws.

GREENWOOD (op. cit.) remarks that 5 fish of 3.7-6.4 cm SL collected during the present investigations from depths of 15-35 m are not morphometrically distinguishable from H. rudolfianus apart from having a single row of teeth in each jaw. There is however a non-quantifiable difference in head shape and a difference in colour pattern. Dr Greenwood believes that these fish may represent a fourth Haplochromis species but requires more material before a proper assessment can be made.

Food: chiefly zooplankton, ostracods and small insects

Breeding: mouth-brooder spawning in sheltered marginal areas of the main lake.

Distribution: endemic to Lake Turkana, restricted to marginal areas close inshore within the 5 metre contour. Chiefly occurs in sheltered situations with macrophytic vegetation, and much commoner on the east shore than on the west. An isolated population lives in Crater Lake A on Central Island.

Commercial importance: nil

Maximum recorded size: 9.5 cm TL

Haplochromis turkanae Greenwood, 1974
(Fig. 5.51)

This species is endemic to Lake Turkana and was first collected during the present investigations. It has proved to be a rare and local species, apparently restricted to the offshore waters of the lake at depths of between 10 and 20 metres.

Description: based on GREENWOOD (op. cit.) covering a size range of 7.3-8.6 cm SL. Length 2.9-3.0 times the maximum depth and 3.0-3.2 times the length of the head. Head length 2.9-3.6 times the eye diameter, 2.9-3.4 times the length of the snout and 3.1-3.8 times the depth of the cheek. Caudal peduncle 1.4-1.5 times as long as deep. Scales in the longitudinal series 31-32. Scales between the upper lateral line and the origin of the dorsal fin 6-7. Dorsal fin rays XIV-XV 9. Anal fin rays III 7-8. Outer premaxillary row of teeth consisting of a mixture of caniniform unicuspids and weakly bicuspids but with 3 or 4 strong dagger-like unicuspids at each end of the posterior ends of the row. Lower jaw with similar mixture of unicuspids and bicuspids in the outer row. Inner series of teeth in both jaws small tricuspids, two rows in lower jaw, three in upper.

Colouration: no accurate description of living fish, but colour pattern certainly inconspicuous.

Formalin-fixed specimens generally pale grey to yellowish grey, whitish below. About five indistinct darker bars on the flanks. Head with conspicuous diagonal black lachrymal bar which extends ventrally onto the lower jaw. Dorsal fin marked posteriorly with 4-6 horizontal rows of black spots, the series extending forwards and coalescing to form vertical streaks. Lappets of dorsal fin black. Caudal fin with dark spots forming vertical bars in the partly closed fin. Anal fin with three pale ocelli. First pelvic fin ray elongated, chalky white.

Food: ostracods noted by GREENWOOD (op. cit.)

Breeding: presumably breeds within the lake

Distribution: endemic to Lake Turkana. At present known only from the type locality at a depth of 16 m on a bottom of mud and rock 5.6 km north west of Porr and from a similar habitat between the 10 and 15 km contours off Kakoi in the northern sector.

Commercial importance: nil

Maximum recorded size: 8.6 cm TL

Haplochromis macconneli Greenwood, 1974

(Fig. 5.52)

An endemic form, first collected during the present investigations, which has proved to be common and ubiquitous in the deeper waters of the lake. The biology of this species has been studied in detail and the results are presented separately (see page 1369)

Description: based on GREENWOOD (*op. cit.*) covering a size range of 2.2-7.7 cm SL. Length 2.8-4.0 times the maximum depth and 2.5-4.0 times the length of the head. Laterosensory canals of the head much hypertrophied with the pores greatly enlarged and bones involved inflated in appearance. This unusual feature is particularly noticeable in the preorbital and preopercular bones. Length of head 2.6-3.8 times the length of the snout, 3.0-4.2 times the diameter of the eye and 3.4-5.5 times the depth of the cheek. Caudal peduncle 1.5-2.2 times as long as deep. Scales between the lateral line and the origin of the dorsal fin 5½-7. Dorsal fin rays XIII-XVI 8-10. Anal fin rays III 7-9. In fish of over 5 cm SL the outer row of premaxillary teeth bicuspid anteriorly, flanked by tricuspid posterior teeth but occasionally the entire row is made up of tricuspids. Lower jaw with a similar outer row but with a higher proportion of tricuspids. Fish of 2-4 cm SL have mainly bicuspid teeth in the outer row of upper jaw with a few tricuspids postero-laterally. Bicuspids also predominate in the lower jaw but a few unicuspid teeth may occur posterolaterally. Inner teeth of both jaws are always tricuspid and small, usually arranged in one row but occasionally in two.

Colouration: pale fawn with slight greenish iridescence on the flanks. Fins colourless with the exception of the anal fin which is marked with three bright yellow spots.

Food: chiefly prawns with minor proportions of insects, gastropods and small demersal fish (see page 1373).

Breeding: mouth-brooder spawning in the deeper waters of the main lake. There was an overwhelming preponderence of females in samples with only two males (3.1 and 3.5 cm TL) identified out of a total of over 1200 fish up to 13 cm length. Females mature at a length of ca 5 cm (see page 1371).

Distribution: endemic to Lake Turkana. A demersal fish ubiquitously distributed throughout the offshore area of the lake below the 20 m contour. Ranging closer inshore under the turbid conditions encountered in the north of the lake during the flood season when recorded from a minimum depth of 9 m. Common in the deepest part of the lake below the 110 m contour.

Commercial importance: nil

Maximum recorded size: 13 cm TL

Family Tetraodontidae

Genus Tetraodon L. 1766

Belonging to an aberrant group of fish with the scales reduced to small erectile spines. The stomach is provided with a sac-like outgrowth which can be filled with water (or air if the fish is removed from water) to distend the belly of the fish into a large sphere. Teeth fused to form a beak consisting of two sharp plates in each jaw separated on the midline by a suture. Fin rays soft. Pelvic fin absent. Dorsal and anal fins short, placed posteriorly one above the other.

Tetraodon fahaka Bennett, 1834

(Fig. 5.53)

WORTHINGTON and RICARDO (1936) reported that although no specimens were collected from Lake Turkana by the 1930-31 Cambridge University Expedition, reliable observers had noted Tetraodon at the south end of the lake. Subsequently both HAMBLYN (1962) and MANN (1964) caught this species in the Ferguson's Gulf area of the lake.

Diagnosis: the generic description which appears above should be sufficient to identify this species in Lake Turkana. The body is usually 3-4 times as long as deep in the uninflated condition. Dorsal fin rays number 11-12 and anal fin rays 9-10. The spines which represent the scales are feeble and slight.

Colouration: yellow with a bold pattern of coalescing dark brown or black stripes on the dorsal surface.

Food: chiefly insects, particularly Anisopteran larvae.

Description: an uncommon species restricted to coastal areas of the lake. Mostly caught onshore or within the 5 m contour but occasionally taken in the trawl on rocky outcrops down to a depth of 16 m. Probably occurs under suitable environmental conditions throughout the lake but the majority of records were from the Allia Bay area.

Elsewhere extends throughout the soudanian region from the Gambia and Senegal through the Volta, Niger and Chad basins to the Nile.

Commercial importance: nil

Maximum recorded size: 26 cm TL

PELAGIC POST-LARVAL STAGES

This section comprises illustrations of examples of the pelagic early stages of fish with notes on their diagnostic characters and methods of identification.

The material was collected by metre townet (mesh size 0.8 mm) during routine sampling in the open waters of Lake Turkana.

Due to the escapement of the earlier stages through the meshes of the net, most specimens obtained were post-larvae between the lengths of 8 and 20 mm. Considerably smaller numbers of post-larvae between 6 and 8 mm were caught, and very few of less than 6 mm TL. Apart from certain exceptions (see below) the smallest post-larvae obtained had already reached a developmental stage characterised by the following features:- yolk sac completely resorbed; swim bladder clearly visible through the body wall above the gut; tail symmetrical in outline; notochord straight but primordia of hypurals and caudal fin rays visible in the ventral fin fold as a keel-like projection near the tip of the notochord; primordia of dorsal and caudal fins faintly visible.

The exceptions were *Synodontis schall* which was frequently obtained in a larval stage with the yolk sac still present, and a small number of prolarvae of *Lates* sp. measuring 3-4 mm TL.

In the smallest larvae size is expressed as total length (TL) as the caudal region is normally rounded at this stage. Most species later develop forked caudal fins and, in these, fork length (FL) is used as soon as it is applicable.

Hydrocynus forskalii Cuv.

(Fig. 5.54)

General diagnosis of post-larva:- body slender, torpedo-shaped; head and eyes moderately large. Jaws and teeth well developed in fish of 10 mm FL and above. Gut markedly elongated, the distance between the snout and the anus approximately 85% of SL. Anal fin short, fin rays III 11-12. Dorsal fin situated on the vertical to the pelvic fins, above the middle of the gut. Number of vertebrae high (ca 48). Pigment sparse, consisting only of a peppering of melanophores on the dorsal surface of the cranium, a rather faint line of about six melanophores along the base of the anal fin and a row of small melanophores along the horizontal myoseptum in the region of the caudal peduncle.

Dorsal and anal fin primordia appear at about 8 mm TL. Pelvic fin buds appear and teeth become apparent on jaws at 10 mm FL. The teeth are initially tricuspid and are later replaced in juveniles by massive interlocking unicuspid teeth.

The length and shape of the body, together with the high number of vertebrae and myotomes prevent confusion between post-larvae of *Hydrocynus* and those of *Alestes minutus*, *A. ferox* and *Micralestes acutidens*. The general shape of the head and body, relative positions of dorsal and anal fins combined with the low number of anal fin rays and scarcity of pigment distinguish this species from *A. baremose*.

Alestes baremose Joannis

(Fig. 5.5 a-d)

General diagnosis of post-larva:- head small, body long and slender with high number of vertebrae and myotomes (47-51 vertebrae); swimbladder rather inconspicuous with only moderately heavy pigment on its dorsal surface; the dorsal and anal fin rays begin to appear at 9 mm TL and a full complement of anal fin rays is formed by a length of 12.5 mm FL; branched anal fin rays high in number (23-27); body and fins extensively peppered with melanophores by a length of 13 mm FL

A. baremose can be separated at small sizes from Engraulicypris stellae and Chelaethiops bibie by the position of the dorsal fin primordium which is well anterior to the anal fin and placed above the hind section of the gut.

It is distinguished from Alestes minutus and A. ferox of less than 12 mm FL by its long slender body, smaller swimbladder, comparately high number of vertebrae and/or myotomes (48-51 in A. baremose cf under 40 in A. minutus and A. ferox) and its characteristic pigment pattern. It can also be differentiated from Hydrocynus forskalii at small sizes by the marked differences in proportions of gut-length to body-length (see Fig.   ) and the position of the dorsal fin in relation to the anus and anal fin.

Above a length of 12 mm FL the large number of branched anal fin rays (22-27) together with the characteristic pattern of pigment on the body and fins distinguish A. baremose from other species, with the possible exception of A. dentex. No recognisable post-larvae of A. dentex were found in metre townet samples but it is likely that they closely resemble A. baremose in pigment pattern. The two species are readily separated by the number of branched anal fin rays (19-22 in A. dentex cf 22-27 in A. baremose). Juvenile A. dentex of 20 mm FL and above which were occasionally obtained in shore samples were separated from A. baremose using these criteria.

Alestes nurse (Rupp.)

Though normally a littoral species, young stages of A. nurse were occasionally taken in townet hauls from close inshore. The post-larvae resemble A. minutus in shape and proportions but differ in pigmentation. Patches of melanophores are present on the dorsal mid-line. This spreads onto the flanks as far down as the horizontal myoseptum in specimens of 14 mm FL and above. At about this length melanophores on the caudal peduncle begin to concentrate to form an indistinct dark patch which appears as a definite black spot in the adult. Though never very intensely pigmented the post-larvae of A. nurse are always distinctly darker than the almost pigment-free post-larvae of A. minutus. In specimens of 15 mm FL and above the profile of the head and snout can be seen to be more rounded and less blunt than that of A. minutus and at the same time considerably less prolonged than in A. ferox.

Alestes minutus Hopson

(Fig. 5.56 a-c)

General diagnosis of post-larva:- eye noticeably large, body moderately elongated and compressed, dorsal part of body cavity occupied by conspicuous swimbladder, 2-chambered in specimens above the length of 11 mm FL, which extends the entire length of the body cavity. The swimbladder is more or less darkly pigmented along its dorsal surface and remains visible through the body wall up to a length of 15 mm FL. Head and body otherwise unpigmented except for a few ill-defined melanophores at the base of the caudal fin rays.

The post-larval stages of A. minutes and A. ferox are not readily distinguishable below a length of 11 mm FL as their morphometric characters overlap and both species lack pigment. At about 11 mm FL differences become apparent in the shape of the head and jaws (Figs. 5.56c and 5.57).

A. minutus is easily separated from A. baremose at all stages by the comparatively low number of vertebrae and/or myotomes (35-39 cf. 48-51 in A. baremose) and, from a length of 11 mm FL, by the low number of branched anal fin rays (12-14 cf. 23-27 in A. baremose). The lack of superficial pigment on head and body also distinguishes the species from A. baremose.

A. minutus is distinguished from Micalestes acutidens by the latter's conspicuous pattern of internal and superficial melanophores, and this distinction also applies to Barilius niloticus.

The positioning of the dorsal fin, well anterior to the anal fin, precludes any confusion of this post-larva with either Engraulicypris stellae or Chelaethiops bibie. Possible confusion, at small sizes, with Hydrocynus can be resolved by reference to Figure 5.54 which demonstrates the differences in proportions of gut-length to body-length and the relative positions of the dorsal and anal fins in the two forms.

Alestes ferox Hopson

(Fig. 5.57)

No post-larvae of less than 11 mm FL were identified. From 11 mm FL and upwards post-larvae of A. ferox were recognized by their characteristically elongated jaws and the somewhat concave profile of the snout. At lengths of 15 mm FL and upwards the dorsal part of the head and body become moderately pigmented. A fine speckling of melanophores develops on the head and dorsal surface of the body and on the dorsal and caudal fins. A dark spot forms on the tip of the snout and frequently an ill-defined dark patch appears on the caudal peduncle.

Micralestes acutidens Peters

(Fig. 5.58 a-c)

General diagnosis of post-larva:- head and eye moderately large; body rather compact and laterally compressed with large coiled visceral mass, often orange-coloured; long, 2-chambered swimbladder extending diagonally from just behind head to anus, heavily pigmented along its dorsal surface and clearly visible through body wall up to a length of 15 mm FL. Development is precocious compared to that of the other local characin species. For example, a speciment of M. acutidens of 8 mm FL has reached a developmental stage equivalent to that reached by the other characins at 9 or 10 mm FL.

Micralestes acutidens is distinguished at small sizes from Alestes minutus, A. ferox and Hydrocynus forskalii by the large orange-coloured stomach and hepatic region together with the heavily pigmented swimbladder.

Precocious development of the unpaired fins facilitates easy separation of M. acutidens from other characins at lengths below 9 mm FL, and from Alestes baremose in particular. The caudal fin of M. acutidens is fully formed, and dorsal and anal fin rays are clearly discernable at 8 mm TL. At a comparable size A. baremose still has a straight notochord, with no development of caudal, dorsal or anal fin rays. In larger post-larvae the features of pigmentation (Fig. 5.58c) together with the relatively low number of anal fin rays, vertebrae and/or myotomes in M. acutidens distinguish it from A. baremose and other species.

In juvenile stages of 14 mm FL and above, M. acutidens is easily separated from A. nurse, a superficially similar species which often occurs in the same samples, by the presence of a conspicuous line of black pigment along the horizontal myoseptum which begins to develop on the caudal peduncle in fish of only 8 mm TL but intensifies and extends forward with increasing age.

Labeo horie Heckel

(Fig. 5.59 a and b)

General diagnosis of post-larva: head large with markedly well-developed lips; small eyes; swimbladder moderately large; head and body well-pigmented with characteristic pattern of melanophores. The pigmentation increases in extent with size. Dorsal and anal fin primordia appear at about 8.5 mm TL. Pelvic fin buds start to develop at 10 mm FL. By a length of 12 mm FL the post-larva shows all the basic adult characters with dorsal, anal, caudal and pelvic fins formed and fin-folds fully resorbed. A fairly dense peppering of small melanophores covers the dorsal part of the head and body extending laterally as far as the horizontal myoseptum. Large peritoneal melanophores in the region of the viscera are visible through the ventro-lateral body wall up to 15 or 16 mm FL. A well-marked narrow line of melanophores runs along the horizontal myoseptum and the dorsal and caudal fins are dotted with fine melanophores.

Barilius niloticus Joannis

(Figure 5.60 a-c)

General diagnosis of post-larva: body long and slender; head small, eye moderately large; pigment sparse except on dorsal surface of swimbladder where it is dense and conspicuous. Barilius niloticus is distinguishable at small sizes from characin post-larvae by the small, rounded swimbladder which is noticeably different from the elongated two-chambered swimbladder of characin post-larvae such as Alestes, Micralestes and Hydrocynus. It differs from Engraulicypris stellae and Chelaethiops bibie most obviously in the anterior position of the dorsal fin. In B. niloticus this is positioned over the hind section of the gut while in E. stellae and C. bibie the dorsal fin lies directly above the anal fin.

At larger sizes B. niloticus can be separated from characin post-larvae by its lack of an adipose fin and the distinctive form of the head.

Engraulicypris stellae Worthington

(Fig. 5.61 a and b)

General diagnosis of post-larva: body slender; head and eyes moderately small; swimbladder compact, more or less darkly pigmented on its dorsal surface; dorsal fin in posterior position, above anal fin. Pigment sparse in post-larvae of less than 12 mm FL, consisting of a few unevently spaced melanophores along base of anal fin and on ventral mid-line of caudal peduncle, one or two melanophores at base of caudal fin rays and a line of about six melanophores on the dorsal surface of the vertebral column extending forward from the urostyle.

From 12 mm FL upwards, additional pigmentation develops on the head, body, and internally on the peritoneum and gill arches (Fig. 5.61b). The peritoneal pigment is dense in post-larvae of 15 mm and above, and this is conspicuous in formalin-fixed specimens. A line of black pigment develops along the horizontal myoseptum in the region of the caudal peduncle, extending forwards as far as the head in adults, as a thick black mid-lateral band.

Engraulicypris stellae post-larvae can be separated from Chelaethiops bibie at all sizes by striking differences in pigmentation pattern (see below and Fig. 5.61b). Other diagnostic features of E. stellae include a comparatively smaller and less heavily pigmended swimbladder, the dorsal fin placed above the vertical to the first branched anal fin ray (cf 4th or 5th branched anal fin ray in C. bibie), smaller pectoral fins and shorter anal fin. These two latter characters are more distinct in larger specimens.

Chelaethiops bibie Joannis

(Fig. 5.62 a and b)

Post-larvae resemble Engraulicypris stellae in shape and proportions but differ strikingly in pigmentation. A conspicuous line of small but well-defined and evenly spaced melanophores extends along each side of the anal fin base uniting posteriorly on the caudal peduncle and continuing as a single row on the ventral mid-line to end on the base of the caudal fin rays. The dorsal surface of the caudal peduncle also bears up to six well-defined melanophores on the mid-line. A series of melanophores extends above the intestine to the anus. The swimbladder is somewhat larger than that of E. stellae and is more darkly pigmented. Cephalic pigmentation is limited to a few large melanophores on the dorsal surface of the cranium. The pectoral fins of C. bibie are relatively longer than in E. stellae and this difference is already apparent by a size of 9 mm FL.

The dorsal fin is set more posteriorly than in E. stellae with the origin lying on the vertical to the 3rd or 4th branched ray of the anal fin. In specimens of 12 mm FL and above, there is no darkly pigmended peritoneum showing through the body wall as in E. stellae, and the mid-lateral line which develops on the horizontal myoseptum is always narrow and comparatively faint.

Synodontis schall

(Fig. 5.63)

Young stages of *S. schall* were the only examples of post-larval siluriform fish to occur in metre townet samples and were mainly less than 9 mm TL, many with yolk-sacs still present.

Diagnosis of larva 6-7 mm TL: head large, body slender and tapering; mouth and lips large and well-developed with conspicuous maxillary barbels; inner and outer mandibular barbels present: characteristic pattern of minute black melanophores on head (Fig. 5.63); large yolk-sac present in anterior ventral position, completely absorbed by about 8 mmTL. Body and unpaired fins under developed in comparison with head; at 7.5 mm TL no dorsal or anal fin primordia visible but primordium of caudal fin beginning to form. Body heavily speckled with minute melanophores. Myotomes 34-38 (modal number = 36). The low number of myotomes would prevent confusion between larval stages of *S. schall* and those of *Bagrus bayad* (53 myotomes), *Chrysichthys auratus* (39-40) and *Schilbe uranoscopus* early juveniles of which, measuring at least 20 mm FL, occurred very occasionally in metre townet samples (Fig. 8.57).

Lates spp.

(Fig. 5.64 a, b, c and d)

Lates post-larval stages were common in metre townet samples from Lake Turkana and appeared identical to the young stages of *L. niloticus* described from Lake Chad (HOPSON, 1969). It was assumed therefore that the young of both *L. niloticus* and *L. longispinis* were represented in the samples, but up to date, no means of distinguishing between the two species, under 4 mm TL, has been found. The illustrations (Fig. 5.64, a, b, c, d) are of larval stages of *L. niloticus* from Lake Chad (from HOPSON, *op. cit.*) and the following notes are given on the assumption that a similar course of development occurs in *L. niloticus* and *L. longispinis* of Lake Turkana.

The eggs are pelagic, averaging 0.83 mm in diameter, with a single large oil globule and narrow perivitelline space. Hatching occurs at an unusually premature ontogenetic stage, 1.2 mm in length. At about 3.4 mm TL the eggs become pigmented, mouth and gill-slits open and feeding begins. At 5.5 mm TL dorsal and anal fin primordia begin to appear, teeth are visible on the jaws, the yolk-sac is almost absorbed and the tail is heterocercal. By 7.2 mm TL the tail is homocercal, dorsal and anal fin-rays formed, primordia of pelvic fins visible as a pair of minute fin-folds on the belly, and pigmentation is assuming a characteristic pattern with 3 longitudinal lines of melanophores conspicuous on the caudal peduncle (Fig. 5.64). At 12.5 mm TL the young fish resembles an adult in shape; well-developed spines are present on the anterior dorsal fin, and mottled juvenile pigmentation is now present (Fig. 5.64). Post-larval stages terminate at between 15 and 17 mm TL when scales are formed.

SUMMARY

Expeditions visiting the region of Lake Turkana, from 1895 onwards collected specimens of fish for scientific study. A brief history is given of their additions to the fauna list up to those of the present survey. The total ichthyofauna now stands at 48 species, of which 30 occur habitually in the lake itself. Only ten of the species are endemic to Lake Turkana

The ichthyofauna is originally derived from the Nile system and clear geological evidence shows that the lake was connected with the Nile basin as recently as 7000 years ago. Of the 48 species, 30 are characteristically soudanian with ranges extending from the Nile to West Africa.

In a comparison between the icthyofaunas of Lake Turkana major and other major African lakes, the closest parallels were found with Lake Mobutu (formerly Lake Albert) where the fauna was also derived from the Nile, and similarly contains a relatively low proportion of endemic species. The probable reasons for this are discussed.

As in Lake Mobutu, the endemic species in Lake Turkana are chiefly confined to the midwater and offshore demersal habitats. _Alestes ferox_ and _A. minutus_ (sympatric species evolved probably from _A. nurse_) together with _Lates longispinis_ are dominant in the midwater community extending throughout the open waters. A fourth endemic species, _Engraulicypris stellae_, occurs abundantly both inshore and in the offshore midwater community.

Three out of four of the species forming the demersal community in deeper waters, _Haplochromis turkanae_, _H. macconneli_ and _Barbus turkanae_, are also endemic.

Most species of fish in the lake tend to be restricted to a particular type of habitat and four major communities of fish were recognized on a basis of habitat preference:-

(a) Littoral
(b) Inshore demersal
(c) Offshore demersal
(d) Pelagic

The boundaries of these communities shift seasonally and are chiefly determined by light climate. The communities and their subdivisions are described.

Spawning habits are discussed briefly and the more important fish are grouped according to the location of their spawning sites.

A brief synopsis of the feeding habits of the principal species of fish is given and it is shown that most food resources are utilized with the exception of the dominant alga of the open lake, _Microcystis aeruginosa_, which is not usually grazed on directly.

Systematic descriptions of each species of fish are provided, with accompanying notes on their ecology, distribution and economic importance.

The chapter ends with a section devoted to the pelagic early stages of fish with notes on diagnostic characters and methods of identification.

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